Sensitivity of mesic temperate grassland to increased climate variability – biomass production, forage quality and plant-plant interactions

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Content

1 Introduction

Global and regional precipitation and temperature patterns are changing due to global warming (IPCC 2014a). Grassland ecosystems are facing not only an increase in magnitude and frequency of extreme weather events, but also the impacts of more variable climate. This thesis is aimed at better understanding the response of mesic temperate grassland to increased climate variability. More specifically, impacts of precipitation and temperature variability on experimental and semi-natural grassland communities were elucidated and their underlying processes were identified. Furthermore, part of this thesis was to test possible management strategies to adapt to the projected climate change, namely fertilisation and variation of cutting frequency and timing. To address these research goals, an experimental approach was applied where precipitation patterns were manipulated in a long-term field experiment. However, climate change experiments have limitations and challenges. Therefore, a critical view on field experiments is given and recommendations are made on how their results can be better integrated into earth system models. Heeding these recommendations, the projections on natural processes and future impacts of climate change might be improved.

Therefore, the main research questions of this thesis were:

Identifying effects of altered precipitation variability: How does increased intra-annual precipitation variability affect productivity, forage quality and plant community composition of mesic temperate grassland?

Interaction of multiple climate factors: Are the effects of increased intra-annual precipitation variability on the productivity and plant composition of mesic temperate grassland amplified when it is co-occurring with seasonal warming?

Investigating underlying processes that alter the resistance and resilience of temperate grassland: What role do plant-plant interactions play for grassland productivity in the face of increased precipitation variability?

Finding adaptation strategies: Does fertilisation and varying cutting dates, or the alteration of cutting frequency, buffer negative effects of increased intra-annual precipitation variability on productivity and forage quality of temperate grassland?

A critical view on precipitation change experiments: How is it possible to improve the integration of biological data from precipitation manipulation experiments into climate change models?

Structure of the thesis:

Chapter 2 gives background information on the (2.1) current knowledge on climate change with a focus on definitions, observations and projections of climate variability. This information underlies the relevance for studying climate change impacts because climate change is still ongoing. The section is followed by (2.2) an overview of evidences of climate change impacts on vegetation, in general, and by a brief presentation of theories on how climate variability might affect vegetation in particular. Afterwards, (2.3) I discuss why mesic temperate grassland was chosen as a study object and present, in detail, current knowledge on its response to increased temperature and precipitation variability. Thereby, the focus lies

on the main response parameters of this thesis: above- and belowground net primary productivity, forage quality, plant-plant interactions, and plant community composition. Section 2.4 highlights mitigation and adaptation as two main response strategies to the projected climate changes. The influence of cutting frequency, cutting date, and fertilisation are discussed as potential adaptation tools. Chapter 2 closes with critical remarks on climate change experiments and how the gap between experiments and models might be bridged. Chapter 3 summarises the content of the six manuscripts which form this cumulative thesis including the declaration of my own contribution. In chapter 4, I present the main findings identified in my research and discuss their contributions in answering the research questions. Furthermore, questions and challenges, which arose as a result of my research, are given in chapter 5. This chapter is followed by the references, which were used in the chapters 1 – 5. The six manuscripts presenting detailed information on the research are given in chapter 7. In addition to the papers presented in this dissertation, I contributed to other studies during my work on this thesis which I have listed in chapter 8. Chapter 9 includes a table of all my presentations given at national and international conferences regarding my work. The thesis closes with summaries in English and German, acknowledgements and declarations.

2 Background of the thesis

2.1 Climate change and climate variability

The Earth's energy budget, and with it the global climate system, is continuously changing (Cubasch et al. 2013). The radiative balance between incoming solar short-wave radiation and outgoing long-wave radiation is affected by natural climate variability such as modulations of the solar cycles, seasonal/ diurnal vegetation and land surface properties, and volcanic eruptions (Cubasch et al. 2013). Furthermore, increasing human activities such as emissions of greenhouse gases and aerosols as well as land use changes altering albedo are having effects on the radiative balance (Cubasch et al. 2013). The Framework Convention on Climate Change (UNFCCC) therefore defines climate change as '*a change of climate which is attributed directly or indirectly to human activity that alters the composition of the global atmosphere and which is in addition to natural climate variability observed over comparable time periods'* (IPCC 2013a). Human activities such as the combustion of fossil fuels, cement production, and deforestation are responsible for the increases in the atmospheric concentration of carbon dioxide, methane and nitrous oxide. This has led to positive global radiative forcing compared to pre-industrial values, and therefore to an unequivocal global warming (Giorgi et al. 2011; Cubasch et al. 2013). In consequence of global warming the hydrological cycle of the Earth is accelerating, thereby increasing climate variability[1]. Thus, precipitation patterns are changing and leading to more frequent and more intense weather events such as extreme drought and heavy rainfall (Hennessy et al. 1997; Trenberth 1999; Allen & Ingram 2002; Trenberth et al. 2003; Giorgi et al. 2011; Collins et al. 2013; Lehmann et al. 2015). Higher temperatures improve the water holding capacity of air and raise the atmospheric water vapour concentration. In combination with altered vertical velocity, this is resulting in an increase of heavy rainfall events (Schär et al. 1996; Trenberth 1999; O'Gorman & Schneider 2009; Kunkel et al. 2013b). Additionally, increasing temperatures support evaporation which reduces soil moisture levels and contributes to severe summer droughts (Briffa et al. 2009). The modification of timing, frequency, intensity, duration, and spatial extent of extreme weather events are of increasing relevance not only for ecological research. They are also highly relevant for climate policies as these modifications are expected to pose stronger threats to society and ecosystems compared to changes in mean precipitation conditions and global trends alone (Easterling et al. 2000b; Hegerl et al. 2004; Jentsch & Beierkuhnlein 2008; Leggewie & Welzer 2010; IPCC 2012; Grimm et al. 2013)

Therefore, in the following sections an overview of observations and projections is given firstly of altered global and regional warming and secondly of precipitation variability with a focus on extreme weather events (drought and heavy rainfall) due to climate change.

[1]"Climate variability refers to variations in the mean state and other statistics (such as standard deviations, the occurrence of extremes, etc.) of the climate on all spatial and temporal scales beyond that of individual weather events. Variability may be due to natural internal processes within the climate system (internal variability), or to variations in natural or anthropogenic external forcing (external variability)." (IPCC 2013a)

2.1.1 Global and regional warming – observations and projections

Observations

The globally averaged surface temperatures (land and ocean combined) have risen by 0.85°C from 1880 to 2012. Furthermore, there have been less cold days and nights, and warm days and nights increased on the global scale (Hartmann et al. 2013). Warming shows also seasonal and regional differences (Jones & Moberg 2003; Xia et al. 2014; Deutscher Wetterdienst 2015; Franzke 2015). Global land-surface air temperature has increased faster in spring and winter than in summer or autumn (Xia et al. 2014). Furthermore, the extreme temperature range has decreased in some locations (e.g. Trondheim/Norway), whereas in others (e.g. Madrid/Spain), it has increased (Franzke 2015).

In Germany, mean annual temperature has increased by 1.3°C from 1881 to 2014 (Deutscher Wetterdienst 2015, Table 1). Depending on the time period observed, warming in Germany seems to be more pronounced during winter (Schönwiese et al. 2005; Jacob et al. 2012) and summer temperatures became more variable (Della-Marta et al. 2007). The warming trend is highest in Bavaria and the Northwest (Lower Saxony, North Rhine-Westphalia, Rhineland-Palatinate, Saarland) with a 1.4°C increase and lowest in the Northeast (Brandenburg, Berlin: 1.1°C) (Deutscher Wetterdienst 2015).

Table 1 Climate trends in Germany according to Deutscher Wetterdienst (2015) for the period 1881-2014 and Schönwiese et al. (2005) for 1971/1981-2000

Climate parameter	Spring	Summer	Autumn	Winter	Year
Temperature (K)					
1881-2014	+1.4	+1.1	+1.3	+1.1	+1.3
1981-2000	+1.3	+0.7	−0.1	+2.3	+1.1
Precipitation (%)					
1881-2014	+11	−0.6	+7.6	+26	+10
1971-2000	+13	+4	+14	+34	+16

Projections

It is unclear, how anthropogenic greenhouse gas emissions will develop in the coming decades. Long-term projections of global climate change for the mid and end of the 21st century are presented within the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC 2013b). These projections are based upon four different emissions scenarios called Representative Concentration Pathways (RCP) ranging from low to high greenhouse gases emission. According to all four RCPs global mean surface temperature will likely increase by 0.3°C to 0.7°C during the period 2016-2035 compared to the years 1986-2005 if natural climate variability remains low (Collins et al. 2013). The global surface temperature for 2081-2100 is projected to increase between 0.3 to 4.8°C depending on the emission scenario used (Collins et al. 2013). There will be regional and seasonal differences in temperature change, such as higher changes over land than over oceans or that greatest warming is very likely occurring in the northern high latitudes (Gillett et al. 2011; Collins et al. 2013). Hot temperature extremes and heatwaves are likely to occur more frequently in Europe, Asia and Australia; cold temperature extremes are expected to become fewer in most places (Collins et al. 2013; Schoetter et al. 2015).

Temperature increases will also be different within Europe. Summer temperatures are projected to increase by 2.5°C between 2040-2050 (relative to 1961-1990) in the Mediterranean, whereas in a large part of Central Europe the expected increase will likely be less than 1°C (Jacob 2009; Wagner et al. 2013). However, winter temperatures will likely increase by 1.5 to 2.0°C from Scandinavia to Mediterranean, and summer temperatures are projected to increase its variability differently across Europe (Fischer & Schär 2008, Figure 1). Up to the end of the 21st century, extreme temperatures will rise faster than moderate temperatures in Central Europe due to higher temperature variability, and the frequency, intensity and duration of heatwaves will increase (Beniston et al. 2007).

For Germany, the mean temperature will likely increase by 1.7°C during the years 2031-2061 (relative to 1981-2010) and 2.4 to 4.9°C by 2100 (Gerstengarbe et al. 2015). Particularly, monthly winter temperatures are projected to rise on average by 2°C and the number of frost days will decrease (Gerstengarbe et al. 2015). Furthermore, the probability for warmer summers and higher summer temperature variability in Germany has increased (Schönwiese et al. 2004; Fischer & Schär 2008; Jacob et al. 2012; Gerstengarbe et al. 2015, Figure 1).

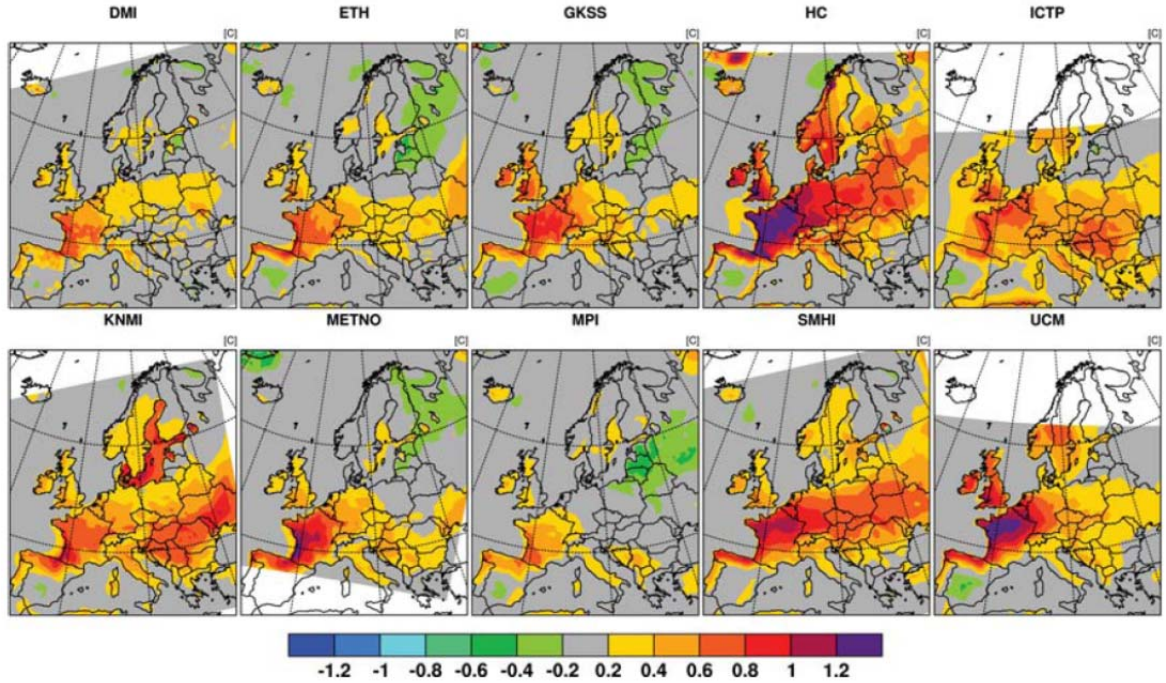

Figure 1 Change in intra-seasonal summer temperature variability (K) simulated by ten different regional climate models (RCM) for the scenario 2071-2100; all RCM show a general tendency towards higher intra-seasonal variability for the projected time period especially over France. Projections for Germany show also increases of summer temperature variability. A small reduction of intra-seasonal variability is given for Northern Europe and Southern Iberian Peninsula (figure from Fischer & Schär (2008))

2.1.2 Precipitation variability and extreme weather events – Definition, observations and projections

Definitions

Equivalent to the definition of climate variability (see above and IPCC (2013a)), **precipitation variability** can be defined as the variation in the mean state, standard deviation and/or occurrence of precipitation. Precipitation variability can refer to all spatial and temporal scales beyond that of individual rainfall events. Differentiation is usually made between interannual and intra-annual precipitation variability. Interannual variability refers to changes in annual precipitation amounts. Intra-annual variability refers to changes in precipitation pattern within a year/season while the annual precipitation amounts remain constant.

Although **extreme weather events** are easily recognised, no unique and universal definition of "extreme events" exists (Stephenson 2008). The relativeness of the concept "extremeness" and the context dependence of the extreme weather events (availability or selection of climate record; climate history, location) are reasons for this lack of a common definition (Stephenson 2008; Smith 2011; IPCC 2012). Furthermore, an extreme weather event is a complex entity with several attributes such as rate of occurrence, magnitude, temporal duration, timing, and spatial scale that makes it difficult to completely described it with a single number (Stephenson 2008). Extremes can also result '*from the interactions between two unrelated geophysical phenomena'* (IPCC 2012). However, accepted descriptions of single extreme weather events are events that have maximum values of certain meteorological variables or values which exceed above or below a pre-existing thresholds/critical levels on a continuous scale (Stephenson 2008; IPCC 2012). A generally accepted fact of an extreme weather event is its rarity at a particular place and time of year. According to the definition in the fifth IPCC assessment report (IPCC 2013a) extreme weather events *'would normally be as rare as or rarer than the 10th or 90th percentile of a probability density function estimated from observations'.* Another definition of extreme weather events arises from a more ecological perspective which includes extremeness in the driver and the response; thus, an extreme weather event can be an occurrence of a statistically rare or unusual event that alters the ecosystem structure and/or function beyond the level of what is considered normal or typical (Smith 2011). However, such a definition based on the response of ecosystems or organisms are problematic due to the spatial and time context dependence of events.

In this thesis, I focused on changed precipitation variability by the experimentally manipulated occurrence of **extreme drought and heavy rainfall events**. Drought is commonly defined as an abnormal local precipitation deficit (Dai 2011; IPCC 2012). Heavy rainfall is generally a large precipitation event with an accumulation rate exceeding a specific and geographically dependent value (AMS 2012). For the severe weather warning, the German Weather Service defines heavy rainfall as a precipitation event with an amount greater than or equal to 25 mm within one hour (Deutscher Wetterdienst 2005). There are two types of approaches to identify or quantify drought or heavy rainfall events. One is the use of indices such as the Plamer drought severity index (PDSI) or the standardized precipitation–evapotranspiration index (SPEI) (Hartmann et al. 2013; Isbell et al. 2015). A second common approach is the extreme value theory to approximate the distribution of annual extremes of precipitation rates (Kharin et al. 2013). In this thesis, drought and heavy rainfall events were calculated according to the extreme value theory based on local

precipitation data for the growing season of the years 1961-2000 (Kreyling et al. 2008a, **Manuscript 4 & 5)**. Drought was defined as the number of consecutive days with less than 1 mm of daily precipitation and heavy rainfall as the prolonged rainfall period with largest precipitation amounts during the growing season. The Gumbel I distribution (Gumbel 1958) was fitted to the annual extremes. Thus, events with recurrences of 100 and 1000 years, respectively, were calculated. This approach was chosen in this thesis, because it considered the local weather history, the rate of occurrence with a defined magnitude, and because it is repeatable and transferable in other places or regions. However, using extreme value statistics for defining extreme weather events is restricted by the time scale of the available local data set. In choosing a prolonged rainfall period instead of maximum single day rainfall events, this thesis took a common Central European meteorological condition, the Vb-track of cyclones, into account. The Vb-track of cyclones, named by van Bebber in 1891, is a constellation of warm and moist air masses that can cause prolonged and abundant precipitation leading to flooding events in Europe (Malberg 2007; Klose 2008). For example, heavy rainfall caused by a Vb track of a cyclone led to severe flooding and destructions along the Elbe River in August 2002 (Malberg 2007). However, single day heavy rainfall events were also considered in **Manuscripts 1, 2 & 3**.

Observations

The changing climate leads to extreme weather events that are unprecedented in their frequency, intensity, spatial extent, duration and timing (Meehl et al. 2000; IPCC 2012). Since the 1950s, changes in extreme weather events have been observed for many parts of the world. Although the high quality climate data sets with a daily resolution which are required for extreme values analysis are lacking for several parts of the world, alterations in the occurrence of several extreme events were detected with varying confidence (Seneviratne et al. 2012; Hartmann et al. 2013). Overall, in more regions the number of heavy rainfall events has likely increased than decreased (Easterling et al. 2000a; Groisman et al. 2005; Seneviratne et al. 2012). Especially in North America and Northern and Central Europe, the frequency and intensity for heavy rainfall events has increased during the last decades (Alexander et al. 2006; Kunkel et al. 2013a; Kovats et al. 2014). In Europe, this increase is most pronounced during winter though changes in summer are also observed with lower inconsistency due to regional and seasonal variations (Alexander et al. 2006; Seneviratne et al. 2012; Zolina et al. 2013). Assessments of past changes in droughts are difficult and partly controversial. Dai (2011) found increases of drought events for wide areas of the world, especially for most of Europe, whereas findings of van der Schrier et al. (2006) and Sheffield & Wood (2008) showed that dryness trends for Northern and Southern Europe are contrasting. However, scientists agree that in particular Southern Europe has experienced more intense and longer droughts. West Africa also shows increases in intensity and duration of droughts, whereas the frequency, intensity and duration of droughts decreased in central North America and North-western Australia (Dai 2011; Seneviratne et al. 2012). In Germany, the precipitation pattern showed larger regional and seasonal variability during the last decades. An increase of the intensity of winter precipitation by 34% (1971-2000, Table 1) was observed which was most pronounced in the northern part of Germany, while the summers demonstrated a trend to drying, with the exception of the southern part of Bavaria where summer rainfall became more intense (Schönwiese et al. 2005; Trömel & Schönwiese 2007, 2008; Zolina et al. 2009; Deutscher Wetterdienst 2015).

Projections

Theoretically, a precipitation event, which is extreme at the present climate, may become more common or rare in the future, it may also increase or decrease in magnitude. This depends on the alteration in the overall distribution of the precipitation variable and on the change at the end of its distribution curve due to climate change (IPCC 2012). For the projections of climate change a variety of models with a huge range of complexity and scales are used. Since the 4th assessment report of the IPCC, climate models have been further developed and improved. However, large-scale patterns of precipitation are still less well simulated than temperature patterns (Flato et al. 2013). The model simulation of extreme weather events has also substantially progressed although the sensitivity of extreme weather events to temperature variability or trends is underestimated in the majority of models (Min et al. 2011; Flato et al. 2013). For the 21st century, global climate models project not only an increase in total precipitation, but also an increasing probability of more frequent and intense precipitation events for most parts of the world (e.g. Northern America, Northern & Central Europe, Eastern Australia, Asia) due to global warming (Schär et al. 1996; Allen & Ingram 2002; Christensen & Christensen 2003; Karl & Trenberth 2003; Hegerl et al. 2004; Groisman et al. 2005; Alexander et al. 2006; Sillmann et al. 2013; Kunkel et al. 2013b; Fischer et al. 2013; Peterson et al. 2014). Droughts are expected to intensify and last longer during the next decades mainly due to increasing evapotranspiration and/or reduced rainfall amounts. However, projections for droughts are not as strong and uniform as heavy rainfall projections and they show high seasonal and regional variations. Regions such as South and Central Europe, central North America, Mexico, Northeast Brazil and Southern Africa will be mostly affected by more intense and longer drought periods. Drought projections for the other regions are inconsistent and of lower confidence because of the lack of observational data for modelling and appropriate dryness definitions and indices (Sousa et al. 2011; Seneviratne et al. 2012; Hewitson et al. 2014; Kovats et al. 2014). Thus, the precipitation pattern across Europe will continue to change in this century with an increase in extremes: Central and Northern Europe will experience higher winter precipitation events, whereas heavy summer precipitation and the frequency of wet days becomes less over most of Europe, especially in the south (Räisänen et al. 2004; Giorgi et al. 2004; Beniston et al. 2007; May 2008; Wagner et al. 2013; Kovats et al. 2014). Particularly for the Mediterranean more intense and longer drought events are projected (Giorgi & Lionello 2008).

Projections for Germany in 2071-2100 show alterations in the precipitation variability with an increase in the intensity and frequency of extreme precipitation events in comparison to the time period 1961-1990, but the long-term annual precipitation amount is expected to remain the same. However, an increase of drought frequency is projected for the north-eastern, south-western, and southern parts of Germany (Schönwiese et al. 2005; Jacob 2009; Pfeifer et al. 2015). Schwarzak et al. (2015) projected also more persistent summer droughts for Central Eastern Germany until 2100. Furthermore, heavy rainfall events will intensify in Germany with high changes in southern and south-eastern parts during winter (KLIWA 2011; Pfeifer et al. 2015; Schwarzak et al. 2015). Additionally, the probability of heavy rainfall events in summer was projected to increase for most parts of Bavaria, the region along the Rhine and Schleswig-Holstein (Schönwiese et al. 2005). However, recent projections show no robust increase of extreme summer precipitation in Germany (Pfeifer et al. 2015).

2.2 Response of vegetation to climate change

The response of vegetation to climate change depends, for example, on the plant species' abilities to adapt either by modification of their physiology and/or seasonal behaviour or by tracking the shifting climate through migration to new territories (Thuiller 2007). Otherwise, the range size of affected plant species will contract or the species will even become extinct (Parmesan 2006). The speed and global extent of climate change pose additional challenges for plant species survival: shifting the distribution area across short distances might take decades or centuries and evolutionary adaptations will likely require several generations and not all plant species might have the required spatio-temporal abilities to adapt, disperse or migrate (Jentsch & Beierkuhnlein 2003; Visser 2008). According to the climatic variability hypothesis (Dobzhansky 1950; Stevens 1989; Gaston et al. 1998), the probability for plant species to adapt by wide distribution rises with the height of the natural climate variability of the plant species' site.

In the following, I give examples of observed impact of global climate change on ecosystems in general. I present theories on how climate variability might affect vegetation. Thereby, I focus on ecological thresholds and vegetation shifts as well as on possible factors influencing the stability of ecosystems against perturbation by increased climate variability such as species and functional diversity or biotic interactions.

Evidences of climate change impacts on global ecosystems

The interaction of the multiple drivers of climate change (e.g. global warming, changing precipitation pattern, increased frequency and intensity of extreme weather events, higher concentration of atmospheric CO_2, altered nitrogen cycle) together with land cover and land use changes is consequently altering the structure and function of the Earth as a system (Vitousek 1994). Climate change has already wide ranging effects throughout global ecosystems (Parmesan & Yohe 2003; IPCC 2014b). Impacts on vegetation are visible on all scales from genetic (Jump et al. 2008) and elemental level (Gargallo-Garriga et al. 2014; Urbina et al. 2015), single plant performance (Reyer et al. 2013) and population dynamics (Gornish & Tylianakis 2013) to ecosystem functions (Jentsch et al. 2011). With the continuing global alterations in climate, the loss of biodiversity (Sala et al. 2000; Chapin et al. 2000; Alkemade et al. 2010), plant species extinctions (Chapin et al. 2000; Thomas et al. 2004; Thuiller et al. 2005; Smith et al. 2009; Alkemade et al. 2010), higher biological invasions (Dukes & Mooney 1999; Kreyling et al. 2008b; Taylor et al. 2012), shifts in community compositions and species ranges (Parmesan 1996; Walther 2000, 2001; Parmesan & Yohe 2003; Thuiller et al. 2005; Midgley et al. 2006; Murphy et al. 2010; Morueta-Holme et al. 2013, **Manuscript 1**), as well as alterations in species interactions (Klanderud 2005; Brooker 2006; Suttle et al. 2007; **Manuscript 4 & 5**), plant phenology (Penuelas & Filella 2001; Sparks & Menzel 2002; Menzel et al. 2006; Parmesan 2007; Jentsch et al. 2009; Nagy et al. 2013) and primary productivity (Ciais et al. 2005; Kreyling et al. 2008c; Barriopedro et al. 2011, **Manuscript 2 & 3**) are expected to become more pronounced. The increased climate variability and higher frequency of extreme weather events is now acknowledged in ecological climate change research as they may be biologically more significant than shifts in average conditions and global trends (Easterling et al. 2000b; Jentsch 2006; Jentsch & Beierkuhnlein 2008; Thompson et al. 2013; Kreyling et al. 2014). However, there is a

research gap on how exactly altered climate variability affects biodiversity and ecosystem functioning and what kind of processes or mechanisms within the ecosystem are altered.

Phenological and physiological processes in the face of altered climate variability

Changes in climate variability can impact plant's phenology and physiology: Phenological processes such as onset of leaf unfolding and flowering are mainly driven by changes in mean climatic conditions foremost temperature (Menzel & Fabian 1999; Menzel et al. 2006), i.e. the temperature conditions two months prior to flowering onset determines shifts in flowering phenology. However, there are interactions with changes in climate variability (Reyer et al. 2013). Early warm spells are advantageous for early successional and opportunistic plant species, however, the risk of damages by late frost events rises (Leuzinger et al. 2011b; Kreyling et al. 2012). Extreme warm spells, drought, and heavy rainfall events can, depending on their timing and duration, for example, advance or slow down leaf maturity, and extend or reduce the flowering period (Buxton 1996; Luterbacher et al. 2007; Jentsch et al. 2009; Menzel et al. 2011). Essential for physiological processes, such as photosynthesis and nutrient uptake, is the availability of water for the plant. Changes in plant-water relations are resulting from higher temperatures and more intra-annual precipitation variability expressed as prolonged dry periods and/or heavy rainfalls (Knapp et al. 2008; Reyer et al. 2013). Reduced soil moisture combined with a high atmospheric demand for plant transpiration could lead to drought stress resulting in productivity losses, changes in the carbon cycle or mortality (Fay et al. 2003; Porporato et al. 2004). An excess of soil moisture due to water logging after heavy rainfall events will affect the oxygen supply to the plant roots (Striker et al. 2005; Bartholomeus et al. 2008). Furthermore, flooding may induce stomatal closure and hence limiting gas exchange and plant growth (Bradford 1983; Chen et al. 2005). The combination of both, wet and dry extremes, are likely harmful for several specialised and endangered plant species, but they may favour generalists (Bartholomeus et al. 2011). Dreesen et al. (2014) showed that repeated water stress in one growing season (two drought events of 25 days or two droughts combined with a heatwave of 10 days) resulted in plant senescence and leaf mortality. These findings suggest that increased precipitation regimes might cause an accumulation of different kinds of water stress for plants and thus may result in the crossing of an ecosystem threshold. Therefore, climate variability, especially the synergistic interaction of weather extremes, may not only change plant performance, vegetation dynamics, and associated ecosystem functions, it may also drive extinctions (Niinemets & Valladares 2006; Reyer et al. 2013).

Ecological thresholds and vegetation shifts

Lloret et al. (2012) introduced a conceptual model of vegetation shifts in response to altered climate variability: increased climate variability and extreme weather events are expected to lead to abrupt vegetation shifts due to induced mortality. In contrast, gradual changes in mean climatic parameters would keep vegetation pattern either stable or would drive successional change in the long term. Furthermore, in some cases vegetation might also remain unaffected under increased climate variability. However, theoretical and empirical evidence exists that also gradual climatic change could lead to abrupt vegetation change when a critical threshold, or so-called tipping point, is crossed (Scheffer & Carpenter 2003; Lloret et al. 2012). An ecological threshold can be defined as the '*point at which there is an*

abrupt change in an ecosystem quality, property or phenomenon, or where small changes in an environmental driver produce large responses in the ecosystem' (Groffman et al. 2006). Extreme weather events can trigger regime shifts by crossing thresholds, and with the rapid climate change the potential for threshold changes increases (Scheffer et al. 2001; CCSP 2009; Peterson 2009). Extreme events primarily affect individuals or populations in their physiology, growth or fitness which will result in no or small effects on ecosystem processes (Smith 2011; Figure 2). However, the extreme event might cascade to higher hierarchical levels such as shifts in plant species abundance and composition, local extinction or invasion of other species into the ecosystem (Kinzig & Ryan 2006; Smith 2011). Once the 'extreme response threshold' is crossed and the function and/or structure of the ecosystem have fundamentally changed, a prolonged return to the previous state is possible but unlikely (CCSP 2009; Smith 2011; Figure 2).

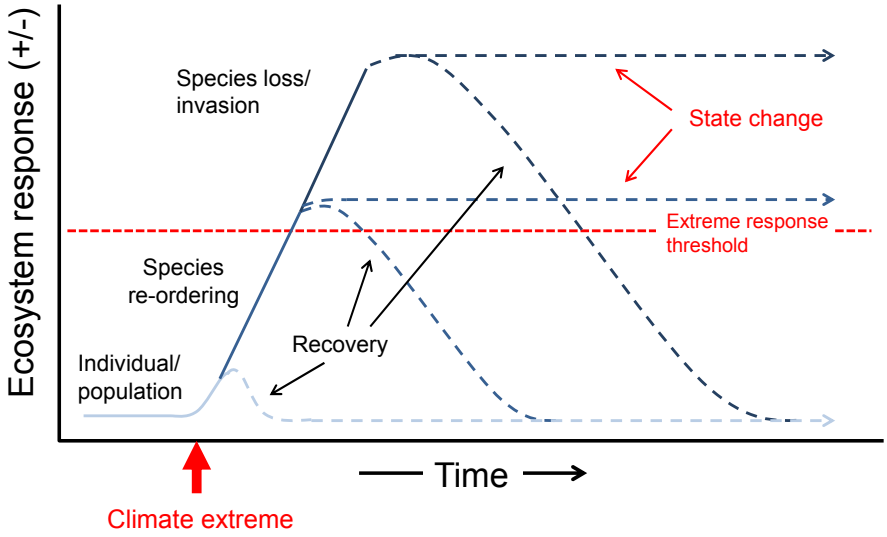

Figure 2 A mechanistic framework for assessing ecosystem response to climate extremes (according to Smith (2011))

According to Lenton et al. (2008) there are indications that some large-scale components of the Earth's system such as the decay of the Greenland ice sheet, the Atlantic thermohaline circulation, or the dieback of the Amazon rainforest, are close to reaching the threshold to a qualitative altered future state of the system due to the global climate change.

Stability of ecosystem functions

Up to now evidences of species or vegetation shifts due to extreme climatic events are still rare, and there seems to be a certain 'stability' of vegetation towards these events (Jentsch et al. 2011; Lloret et al. 2012). Talking about 'ecological stability' can be confusing as there are many definitions of and concepts on stable ecosystems (Grimm & Wissel 1997). For example, a stable ecosystem can be defined as a system that persists despite perturbation (Connell & Slatyer 1977). However, ecosystem stability has several aspects e.g. one focussing on the existence of function or, in contrast, one that focus on the efficiency of function (Holling et al. 1997). From 163 reviewed definitions, Grimm & Wissel (1997) were

able to condense the term ‘stability’ to three fundamentally different properties: (1) constancy, staying essentially unchanged; (2) resilience, returning to the reference state (or dynamic) after a temporary disturbance; and (3) persistence, continuance through time of an ecological system. According to Isbell et al. (2015), the first property ‘constancy’ can also be called ‘resistance’, which indicates that an ecosystem function (e.g. productivity) remains close to the reference state during a climate event. Grimm & Wissel (1997) also introduced a checklist about ecological stability which could reduce confusion. They point out that the stability properties should be addressed correctly in the statements on stability. Furthermore, they recommend to always classify the ecological situation by giving information on the variable of interest, the level of description, the reference state, disturbance, spatial scale, and temporal scale (Grimm & Wissel 1997). Therefore, when the term “stable” ecosystem is used in this thesis, it refers usually to a grassland ecosystem which provides a resilient and efficient ecosystem function in the face of increased climate variability. Here, ecosystem functions are for example biomass production, high forage quality, or constant plant species composition. The reference state would be the lack of extreme weather events and low intra-annual climate variability. The spatial scale ranges from plot size and the size of a meadow, the temporal scale is between one growing season up to 10 years.

What are the processes and the mechanism that keep ecosystem functions stable in the face of perturbation caused by climatic extremes? Before answering this question, we must confirm that the lack of response in plant performance results from the plant’s resistance and not from a lack of true extremeness (Smith 2011). For example, an extreme drought occurs, but the soil moisture content is not reflecting the same level of extremeness because of buffering effects (compare Glaser et al. 2013). Thus, the plant response would not be extreme itself because the event lay within the natural variability of soil moisture availability and therefore within the ability of the plant to cope (Smith 2011; Lloret et al. 2012, Figure 3a). This might easily happen if the definition of “extreme climatic event” is not adequate (Smith 2011; Section 2.1.2).

In the following, concepts on species and functional diversity, biotic interactions, demography of plant species population, ecological stress memory, and their role for ecosystem stability under climate variability are shortly presented.

Species and functional diversity

One acknowledged key mechanism for providing a stable ecosystem function (e.g. biomass production) despite perturbation is a high diversity of species and functional groups (Walker 1995; Naeem & Li 1997; Yachi & Loreau 1999; Hooper et al. 2005). Because species differ in their responses to environmental changes such as increased climate variability, higher species richness offers a wider range of species responses to perturbations (Van Ruijven & Berendse 2010). Thus, more diverse ecosystems have a higher chance to include species that respond with increased performance to the change, compensating the failing performance of other species. This provides a so called ‘insurance’ for maintaining the original ecosystem function (Walker 1995; Folke et al. 1996). Species and functional group richness can also enhance the capacity of the ecosystem to recover from the perturbation; thus, increasing resilience, and potentially offering an opportunity to deal with changes (Walker 1995; Van Ruijven & Berendse 2010).

Biotic interactions

Another possible process for stabilizing ecosystem function in the face of increased climate variability may be the reciprocal feedback between individual species selection and persistence, resulting in alterations in biotic interactions and dominance shifts (see also section 2.3.3 and **Manuscripts 1, 4 & 5**). According to Walker et al. (1999) and Brooker (2010) an environmental pattern, such as extreme weather events or increased climate variability, could favour a particular suite of species leading to a decline or elimination of the dominant species. Thus, the formerly intense competition between the dominant and minor species would decrease and the minor species might emerge to replace the dominant. If the minor species has similar or congeneric functional attributes as the former dominant, the ecosystem function can be maintained under the changed climate regime (compare with 'insurance hypothesis' Folke et al. (1996) and Yachi & Loreau (1999)). Recently, Gellesch et al. (2013) reviewed findings on biotic interaction in the face of climate change. They found that the effect of more than one climatic driver on biotic interactions is especially not yet well understood.

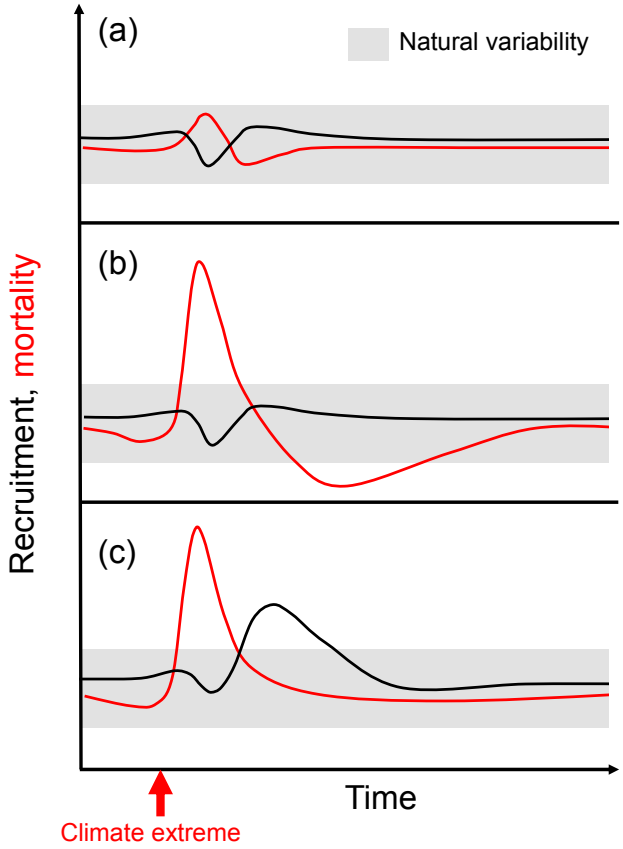

Figure 3 Model of a demographic stabilizing mechanism within populations against extreme climatic events based on compensation by either enhanced survival (b) or increased rate of recruitment (c) after the event caused a higher mortality rate than natural variability; (a) the effect of the climatic extreme does not necessarily cause higher mortality or recruitment rate as alterations fall within the range of natural variability; red lines show rate of mortality, black lines show rate of recruitment (modified from Lloret et al. (2012))

Demography

A further perspective on ecosystem stability in the face of climate variability is a demographic stabilizing mechanism. This mechanism can be based on the balance between the adult mortality of at least one dominant species population induced by an extreme weather event and its enhanced recruitment or adult survival after the event (Lloret et al. 2012). This mechanism could also explain why short-term responses in community composition were found to differ from long-term observations in a warming experiment (Hollister et al. 2005). In the demographic stabilizing mechanism by Lloret et al. (2012), an extreme weather event might cause higher mortality than natural variability (Figure 3b, c). After a certain time, this mortality is compensated by higher survival of the remaining population (Figure 3b) and/or by increased recruitment (Figure 3c). Possible factors which enhance higher survival under or after extreme weather events were named to be site quality, tolerance, plasticity and phenotypic variability as well as reduced competition with plant neighbours. Factors increasing future recruitment could be, for instance, micro-climatic shifts, new suitable sites, better adult reproductive performance, and altered biotic interactions such as less competition, facilitation, and antagonistic release (Lloret et al. 2012). This kind of altered conditions are often brought about by superimposed disturbances (Kröel-Dulay et al. 2015).

Ecological stress-memory

Moreover, there are also evidences that grassland ecosystems show a kind of memory effect to pre-exposure by extreme climatic events such as drought, frost or heat waves (Bruce et al. 2007; Walter et al. 2011, 2013b), which improve the tolerance to further drought stress. Walter et al. (2011) showed that drought-stressed *Arrhenatherum elatius* showed improved photoprotection and therefore a more protective response towards recurrent drought. Together with colleagues, I found that recurrent mild drought stress seemed to improve drought resistance of grassland plant communities and species (Backhaus et al. 2014a). An extreme drought event caused higher tissue die-back of single plant species (*Plantago lanceolata*) and of grassland communities (consisting of *Arrhenatherum elatius, Holcus lanatus, Plantago lanceolata and Geranium pratense),* which were regularly watered in the preceding years, compared to plants that were pre-exposed to only mild or severe drought stress. Here, morphological changes such as altered root-shoot ratio did not cause this response. However, epigenetic changes (Bruce et al. 2007), the accumulation of proteins and transcription factors (Baniwal et al. 2004) or protective metabolites (Herms & Mattson 1992) as well as soil biotic legacies (Meisner et al. 2013) could be potential reasons for these findings. Future research, especially on the molecular level, has still to elucidate mechanisms of an ecological stress-memory.

In summary, the multiple drivers of climate change are altering ecosystems worldwide. Particularly increased climate variability is impacting plant's phenological and physiological processes e.g. via the higher magnitude and frequency of extreme weather events or via the combined occurrence of both, wet and dry extreme events. As a consequence, abrupt vegetation shifts are expected when ecological thresholds are crossed. Processes and mechanisms that might keep ecosystem functioning stable in the face of perturbations caused by climatic extremes are not yet completely researched and understood. Some evidence suggests that biodiversity, biotic interactions, demographic processes of populations, and an ecological stress-memory are able to influence the resistance and resilience of plant communities. Thus, it is important to close the research gap on how

altered climate variability affects biodiversity and ecosystem functioning and to empirically and theoretically identify potential ecosystem thresholds before they are actually crossed. Plant species composition (species and functional diversity) (see **Manuscript 1**) and plant-plant interactions (e.g. facilitation, role of nitrogen fixing plants) (see **Manuscript 4 & 5**) in the face of increased climate variability should especially be further studied as they possibly have a mitigating role to climate change effects. Furthermore, land use forms and management strategies might influence the direction of vegetation response. Therefore, land use practices have to be tested for interactions with climate factors (see **Manuscript 2 & 3**). In future, the interplay of plant-soil-processes and the influence of biotic interactions across different trophic levels should also be considered. In the following, the focus is placed on the response of mesic temperate grassland as one exemplary ecosystem affected by increased climate variability.

2.3 Importance of mesic temperate grassland and its response to increased climate variability

The focus of this thesis lies on mesic temperate grassland ecosystems. Grassland ecosystems support human, fauna, and flora populations worldwide. They provide numerous goods and services; for instance the provision of genetic variability for food grain, forage for livestock, wildlife habitats, biodiversity conservation, resource storage, prevention of soil degradation as well as the support of recreational activities (White et al. 2000). Grassland ecosystems cover about 20% to 40% of the Earth's land area, depending on the definition of 'grassland' (Singh et al. 1983; Sala et al. 1996, 2001; White et al. 2000; Dixon et al. 2014). For example, Singh et al. (1983) defines 'grassland' as natural or semi-natural herbaceous formations, which are dominated by graminoid plants and which can include scattered or clumped woody plants. According to Sala et al. (1996), shrubs often provide this woody plant component in temperate and subtropical regions. Following the definition by White et al. (2000), grasslands are terrestrial ecosystems which are dominated by herbaceous and shrub vegetation and which can encompass non-woody grasslands but also woodlands, shrublands, and tundra. In temperate Europe, forest should be the most abundant 'natural vegetation', however, permanent grassland has developed over many centuries due to moderate disturbances by management in the form of grazing and mowing for hay or silage (Pärtel et al. 2005). This is also the reason why it is often called 'semi-natural' grassland. To conserve these grassland ecosystems in Europe, persistent management is needed (Rieder 1983). Especially in Europe's temperate and humid regions, hay meadows (Figure 4) are of high importance for agriculture (Eurostat 2015).

Figure 4 Hay meadow in Southern Bavaria, Germany (Foto: Grant)

In general, grassland ecosystems are dynamic. Besides temperature and precipitation as the major factors controlling ecosystem processes and grassland distribution; fire, grazing, and land use play important roles (Sala et al. 1996, 2001; Unger & Jongen 2015). These factors provide selective pressure for a high turnover of aboveground plant organs, a short ruderal life cycle involving early reproduction with a high number of seeds, high belowground carbon allocation and the location of perennating organs near the soil surface (Sala et al. 1996; Unger & Jongen 2015). Different grassland management (grazing versus mowing) can further influence soil carbon sequestration through varying proportions of senescent leaf tissue returned to the soil (Sanaullah et al. 2011). In addition to their importance and wide distribution, grassland ecosystems already played a key role in experimental research on

biodiversity because the relatively small size and short life span of grasses is ideal for manipulative and mostly short-term experiments (Sala et al. 2001; Fraser et al. 2015). Thus, they offer good conditions for climate change research studies.

Conceptual differences in the response to more extreme precipitation variability have been stated for xeric, mesic, and hydric systems, which can apply to grassland ecosystems (Knapp et al. 2008; Sala et al. 2015). Here, I only present the response of mesic systems: under ambient precipitation conditions with frequent small and intermediate events, mesic systems are characterized by relative abundant soil water availability and are seldom stressed for most parts of the growing season. They can be defined by a precipitation-evapotranspiration ratio larger than 1 (Knapp et al. 2008). A more extreme precipitation regime with larger, but fewer events would increase plant water stress in mesic systems, because it increases the variability of soil water content. Thus, the soil water level might drop below stress thresholds more often (Knapp et al. 2008). Using a process-based ecosystem model, Sala et al. (2015) simulated water losses and soil-water availability for mesic and xeric sites under increased precipitation variability. They found that soil water availability decreased in mesic sites in contrast to xeric sites due to enhanced precipitation variability. Furthermore, findings of Heisler-White et al. (2008, 2009) confirm this assumption for grassland as they found a 30% increase in aboveground net primary productivity (ANPP) in a semi-arid steppe but a 18% reduction of ANPP in a mesic tallgrass prairie due to increased precipitation variability. Furthermore, Gerten et al. (2008) showed that net primary productivity at hydric sides were least responsive to any change in precipitation compared to xeric or mesic sites.

Thus, grasslands' ecological and economic importance, their good qualities for experimental research as well as their expected high susceptibility to increased variability of precipitation and temperature make mesic temperate grasslands an interesting and important study object. Therefore, in the following sections, the response of mesic temperate grassland to increased temperature and precipitation variability is outlined with a focus on above- and belowground net primary productivity, forage quality, plant-plant interactions, and plant community composition because they are the main response parameter of this thesis. Thereby, findings are separated, if possible, into sections on the effects of extreme drought and heavy rainfall events, interannual or intra-annual precipitation variability followed by temperature effects and the interaction between warming and precipitation variability.

2.3.1 Plant productivity

Aboveground net primary productivity:

Observational and experimental evidences of single drought and heavy rainfall events show controversial effects on aboveground net primary productivity:
Drought: In general, large-scale droughts were shown to reduce terrestrial net primary productivity (NPP) in the Southern and Northern Hemisphere (Zhao & Running 2010, 2011). A Europe-wide reduction of 30% net primary productivity was caused by the drought event in 2003 (Ciais et al. 2005). Considering mesic temperate grassland systems, Grime et al. (2000, 2008) found 34% to 49% reductions of the total aboveground biomass after a drought event compared to control conditions. Gilgen & Buchmann (2009) studied mesic temperate grassland systems at different altitudes and annual precipitation amounts. The sites with

lower annual precipitation (975 mm) were more vulnerable to summer drought and showed decreased aboveground net primary productivity (ANPP), whereas more humid sites in the subalpine region (1534 mm) were not negatively affected by drought. However, despite tissue die-back and reductions of single plant species biomass within mesic temperate grassland communities in some years, the grassland ANPP remained surprisingly stable in the long-term (2005-2010) EVENT I experiment (Figure 5) with annual recurrent drought events (Kreyling et al. 2008a; b; Jentsch et al. 2011, **Manuscript 4**).

Heavy rainfall: Impacts of heavy rainfall events are less studied than drought effects on mesic temperate grassland. Comparable findings were made for the effects of single or annual recurrent heavy rainfall events: ANPP of mesic temperate grassland communities remained stable in the face of seven years with annual recurrent heavy rainfall events (unpublished data from EVENT I experiment, 2005-2011, Jentsch et al. in preparation) except an increase during the very dry year 2008. Although a significant tissue-die back was caused on a community level, heavy rainfall events decreased ANPP only in single grassland species depending on the community composition (Kreyling et al. 2008a, **Manuscript 4**).

Interannual precipitation variability: Large precipitation events coinciding with severe waterlogging or droughts are threats to grassland productivity. However, this is not the only factor. There is growing evidenc that inter- and intra-annual precipitation variability plays a decisive role for alterations in grassland functioning. The variation of interannual precipitation amounts is positively correlated with the variation in ANPP of many terrestrial systems (Hsu et al. 2012). Observations showed that ANPP of the grassland biomes was more strongly affected than the productivity of other biomes (Knapp & Smith 2001). A 6.3% increase of ANPP variability is shown to be caused by a 5% increase in interannual precipitation variability for grasslands (Hsu & Adler 2014). Ecosystems likely have different sensitivity to the interannual precipitation variability due to differences in vegetation structure, biogeochemistry, and in the life history traits of the dominant species (Heisler-White et al. 2009). According to Hsu et al. (2012), the sensitivity of ANPP to varying precipitation mean peaks at sites with average annual precipitation between 300 and 600 mm. However, a North-American mesic temperate grassland was quite responsive to the altered water availability under a wide range of precipitation levels. 40% of the interannual variability in its ANPP could be attributed to the interannual changes in precipitation (Knapp et al. 2001). Interestingly, there seems to be a time lag (one to several years) in the response of grassland productivity to the years with higher precipitation amounts. This results in increases of ANPP as well as the recovery of reduced productions due to previous dry years (Lauenroth & Sala 1992; Oesterheld et al. 2001). This time lag in the response of grassland productivity might be due to low growth rates of dominant grassland species in dry regions, which are therefore not able to respond quickly to changed precipitation patterns (Byrne et al. 2013). Furthermore, the higher growth rates of species in wetter regions could be limited by other resources such as light and nutrients (Byrne et al. 2013). Ecosystems – also grasslands – seem to be able to adjust their water use efficiency (WUE = the ratio of the rate of ANPP to the rate of evapotranspiration). The WUE can increase in drier years and be minimized in wetter years resulting in a tolerance to low annual precipitation amounts (Ponce Campos et al. 2013).

Intra-annual precipitation variability: Not all variations in ANPP results from interannual changes of precipitation. The intra-annual precipitation, also called within-seasonal pattern of precipitation, contributes to large changes in grassland productivity (Lauenroth & Sala 1992;

Nippert et al. 2006; Hsu et al. 2012). Increased intra-annual precipitation variability, expressed by altered timing and frequency of rainfall events, can result in longer dry periods followed by intense rain events. Thus, the variability of soil moisture content is increased which leads to recurrent plant water stress and reduced ANPP (Knapp et al. 2002; Zhang et al. 2013). This kind of precipitation pattern was shown to reduce ANPP of mesic temperate grassland by 10 to 18% (Fay et al. 2000, 2003; Fang et al. 2005; Heisler-White et al. 2009, **Manuscript 2**). In contrast, a shift from low to high variable precipitation pattern with few, but large precipitation events had no effects on the ANPP of mesic temperate grassland in a study by Wilcox et al. (2015). Robertson et al. (2009) and Wilcox et al. (2015) pointed out that it is necessary to understand the species and functional group response to increased intra-annual precipitation variability because they probably influence the alterations in total ANPP. I followed this question in **Manuscript 1**. Hsu et al. (2012) stated that projected changes in interannual precipitation variability will likely have negligible effects on mean ANPP. However, they expect that ANPP will be more sensitive to higher intra-annual variations of precipitation. **Manuscript 3** gives evidence for this statement: **Manuscript 3** revealed that the effects of intra-annual variation in precipitation on ANPP were stronger in years with low precipitation amounts and thus correlated with interannual precipitation variability. Therefore, the increase of both inter- and intra-annual variability of precipitation seems to be a stronger modifier of grassland performance.

Temperature variability: In addition to the threat of increased precipitation variability on grassland performance, especially in productivity, are the impacts caused by the accompanied rise in global temperature. Generally, the increase of air temperatures alone showed a positive effect on photosynthesis and plant productivity (Rustad et al. 2001; Wu et al. 2011).

Interaction of warming and precipitation variability: However, the interaction of warming and precipitation variability could pose a challenge for grassland productivity. Experimental warming was found to stimulate aboveground net primary productivity during cooler parts of the growing season. Negative effects on ANPP occurred when warming induced additional moisture stress on already warm or water-limited periods within the year (De Boeck et al. 2007; Hoeppner & Dukes 2012; Schuerings et al. 2013). Aboveground biomass production of a mesic temperate grassland decreased by 29% due to experimental warming (+3°C) combined with drought stress in the summer (De Boeck et al. 2008). Evidences for the interactive effects of warming and altered precipitation (increases of annual amounts or years with droughts) on ANPP exist (Wu et al. 2011; Hoeppner & Dukes 2012). In contrast, **Manuscript 1** revealed that the effects of increased intra-annual precipitation variability combined with experimental summer or winter warming on ANPP were additive.

Figure 5 View from an irrigated grassland plot on the manipulation equipment of the EVENT-1 experiment: drought events were manipulated using rainout shelters, and irrigation bikes were used for simulation of heavy rainfall (Foto: EVENT archive)

Belowground net primary productivity:

The focus of climate change studies lies mostly on aboveground responses of plants (Byrne et al. 2013). This is probably due to the often destructive and also time or money consuming methods to sample or measure roots, which is not realisable in long-term experiments due to their non-destructive nature. However, belowground processes are important, especially since temperate grasslands can allocate up to 80% of the total net primary production belowground (Gill & Jackson 2000; Byrne et al. 2013).

Drought: Studies about the effects of extreme drought or heavy rainfall events on belowground net primary productivity (BNPP) (or root length as a proxy for BNPP) are similarly controversial to the findings on effects on ANPP. In a greenhouse experiment, reduced water availability caused a reduction of root biomass of a single plant species common for mesic temperate grassland (Weißhuhn et al. 2011). In contrast, BNPP was increased after drought in an otherwise wet and cool summer (Hoeppner & Dukes 2012). Drought was shown to alter the biomass proportioning in favour of root growth allowing the exploitation of reduced soil moisture levels (Kalapos et al. 1996). Thus, the number and total length of lateral roots was increased by drought (Jupp & Newman 1987). However, other studies found that BNPP in mesic temperate grasslands was not significantly altered by single droughts or annual recurrent drought events (Kreyling et al. 2008d; Gilgen & Buchmann 2009; Jentsch et al. 2011; Backhaus et al. 2014a).

Heavy rainfall: Water logging following heavy rainfall events is expected to cause the inhabitation of root growth (Irving et al. 2007) and therefore reductions in BNPP. However, Kreyling et al. (2008d) found no change in root length and root biomass after a heavy rainfall event. Furthermore, in the long-term experiment EVENT I BNPP of mesic temperate grassland remained stable across 7 years with annual recurrent heavy rainfall events. The only exception was a decrease in one year (unpublished data, Jentsch et al. in preparation).

Interannual precipitation variability: Considering the effect of interannual precipitation variability on BNPP, dry years were found to reduce root increments and BNPP of mesic temperate grasslands and the decrease in root increments seemed to have a linear correlation with decreasing precipitation (Fiala et al. 2009, 2012). A study by Frank (2007) revealed, that 2 years of declining moisture reduced temperate grassland BNPP in the upper 20 cm of soil by 39% and by 70% in 20-30 cm depth of the soil. In addition, more annual precipitation was shown to generally increase BNPP or terrestrial ecosystem by 11% (Wu et al. 2011). However, BNPP of temperate sub humid grassland was not altered by 50% reductions or 61% addition of growing season precipitation in the first two years of the study, but was reduced by both precipitation treatments in comparison to control in the third year of the study (Byrne et al. 2013).

Intra-annual precipitation variability: Higher soil moisture variability due to increased intra-annual variation of precipitation could also lead to impacts on BNPP. However, only two other studies (Fay et al. 2003; Padilla et al. 2013) were found in the web of science, besides **Manuscript 2 & 3**, which looked at this topic in mesic temperate grassland: none of these four studies found decreases in BNPP due to increased intra-annual precipitation variability. Padilla et al. (2013) found that grasses and dicotyledons had significantly higher root length under pulsed watering. Fay et al. (2003) showed a 35% increase of the root-shoot ratio caused by small, not-significant decrease of ANPP and increase in BNPP due to the higher soil water variability in the altered precipitation timing treatment.

Temperature variability: Although terrestrial BNPP in general was shown to increase under warming by 52% (Wu et al. 2011), BNPP of a mesic temperate grassland was not affected by year-round warming with infrared heaters up to 4°C (Hoeppner & Dukes 2012). However, Hutchison & Henry (2010) showed that winter-only warming and year-round warming resulted in increased root biomass. This result indicated that the variability of temperature can alter BNPP, because the winter warming with an earlier start into the growing season, and not the higher temperatures during summer, caused the biomass increase. Schuerings et al. (2013) showed that the absence of frost due to warmer winter temperature did not alter total root length, but changed the distribution of roots within the soil profile.

Interaction of warming and precipitation variability: Furthermore, the interaction of variation in warming and precipitation seems to be not only decisive for ANPP, but also for BNPP. BNPP was decreased by 25% as the consequence of the combined warming and summer drought (De Boeck et al. 2008).

In sum, there are similarities in the response of ANPP and BNPP to altered precipitation patterns e.g. a general increase with warming but a decrease when warming coincides with drought stress in summer. However, for both response parameters, findings on effects of single extreme weather events are still controversial. Furthermore, the influence of the interactive effects of altered temperature and precipitation variability on both parameters is not well studied yet. For understanding possible processes behind the impacts of climate change on plants, belowground processes should not be neglected. Only the combination of both might reveal already existing vegetation changes as demonstrated by Fay et al. (2003): no significant alterations were caused in ANPP and BNPP, but the root-shoot ratio uncovered vegetation response to altered precipitation timing.

2.3.2 Nutritive values of grassland - Forage quality

Besides alterations in the productivity of grassland, more extreme precipitation regimes seem to have the ability to change plant physiological processes and nutrient availability (Jentsch et al. 2011), which can lead to decreases in the quality of grassland forage. Lower quality of grassland forage might have huge consequences for grass-fed livestock productions (Buxton 1996; Olesen et al. 2011). Because the demand for food, and thus forage of high quality, is rising with the increase of the world population, direct and indirect impacts of projected altered precipitation regimes on forage quality have to be studied in detail to meet animal requirements (Buxton 1996; Craine et al. 2009; Olesen et al. 2011). Craine et al. (2009) stated that to predict the impacts of climate change on grazers, inter- and intra-annual variation of precipitation on both grassland quantity and quality have to be studied.

General factors influencing forage quality: Major important factors influencing grassland forage quality are temperature, water, and nutrient availability as well as plant maturity, plant species identity, and plant species composition (Buxton 1996; Ball et al. 2001; Bruinenberg et al. 2002; Craine et al. 2009). Forage quality decreases with advancing maturity, because the protein nitrogen and soluble carbohydrates in leaves and stems decline with age (Collins & Casler 1990; Buxton 1996). Furthermore, the plants become more fibrous as the plant ages and the proportion of stems (which have lower protein contents than leaves) increases altering the leaf-to-stem ratio (Buxton 1996; Ball et al. 2001). The fibrous parts are more difficult to digest than the non-fibre components of the plant, therefore also the digestibility of plants is declining with plant maturity (Ball et al. 2001). Not all plants have the same forage quality even at the same maturity stage (Baumont et al. 2008). For example, legumes have less fibrous parts than grasses and produce higher quality forage (Ball et al. 2001). Thus, the botanical diversity influences the quality of the grassland due to the species-specific nutritive values, different ages of leaves and tillers, and the varying maturity stage of each species at the harvest date (Bruinenberg et al. 2002; Baumont et al. 2008). This is also the reason why extensively used and more diverse grasslands revealed lower forage qualities in terms of higher cellulose content, less nitrogen and phosphorus concentrations than a grassland which had less species richness due to an intensive management (Jeangros & Schmid 1991).

Drought and heavy rainfall: Küchenmeister et al. (2014) found that drought had small or inconsistent effects on forage quality. However, their results revealed that plant composition largely determined the nutritive value of the grassland biomass. Both factors, plant maturity and plant species composition, might be altered by climate change and are therefore able to indirectly affect forage quality. Halim et al. (1989) showed that water stress can slow down plant maturity. Thus, if a moderate drought takes place and does not lead to high leaf loss, forage quality might be maintained or slightly improved (Buxton 1996). However, long lasting and extreme drought events are able to inhibit tillering and branching. Additionally, they likely accelerate the death of tillers and senescence of leaves causing the relocation of proteins and carbohydrates from leaves to roots (Buxton 1996; Durand et al. 2010). Furthermore, high water stress can decrease the nitrogen concentrations in the leaves due to lower nitrogen uptake or reduced use of soil mineral nitrogen (Craine et al. 2009; Durand et al. 2010). Long lasting waterlogged soils after heavy rainfall events might also induce nutrient deficiency or toxicity for plants due to the anoxic conditions in the soil (Steffens et al. 2005) and cause a decline in forage quality.

Temperature variability: The rising temperature due to global change will likely have an additional impact on forage quality. Higher temperature usually cause lower quality forage, because of enhanced plant maturity, increased lignification, and reduced leaf-to-stem ratio (Buxton 1996).

Interaction of warming and precipitation variability: The interaction of increasing temperature and decreasing precipitation is especially likely to reduce crude protein and digestible organic matter in grassland. Craine et al. (2010) projected that a 1°C increase would require about 200 mm of additional annual precipitation to maintain the same grassland forage quality and that the additional projected increase of atmospheric CO_2 might further intensify these negative effects.

Intra-annual precipitation variability: Furthermore, the intra-annual variation in temperature and precipitation might be even more important for forage quality. Increased temperatures during spring growth might advance maturity and consequently decrease forage quality more rapidly than during summer growth (Buxton 1996). To my knowledge, there are not any other published studies besides the two of my colleagues and I (**Manuscript 2 & 3**) which look at the direct effects of more extreme intra-annual precipitation variability on forage quality in mesic temperate grassland. However, alterations in forage quality due to increased precipitation patterns can be expected as they were shown to change the metabolism of grasses (Gargallo-Garriga et al. 2014), decomposition of grass material (Walter et al. 2013a), and soil enzyme activities (Schloter et al. 2012). Additionally, changes in nutrient cycles and carbon turnover by increased intra-annual precipitation variability were shown (Knapp et al. 2002). These evidences suggest indirect effects on forage quality via higher variability in water availability, nutrient cycles and plant physiological processes.

2.3.3 Plant-plant interaction and plant community composition

Plant-plant interactions, such as competition and facilitation, affect the establishment, abundance, and distribution of plant species and are one of the processes by which climate change can alter plant community composition (Davis et al. 1998; Brooker 2010; Volder et al. 2010). Usually all species within a plant community compete for the same resources (e.g. water, light, nutrients, space) and only minor differences among species' environmental requirements enables species to coexist (Tilman 1982). Through amelioration of the environment, species can facilitate the coexistence, establishment, growth or invasion of other species (Brooker et al. 2008; Gross et al. 2013). For example, legumes have no need to compete for soil nitrogen due to their ability to fix atmospheric nitrogen and they can promote neighbouring plants by increasing soil nitrogen (Pirhofer-Walzl et al. 2011, **Manuscript 5**). Some plants can also have a nursing effect on their neighbours by providing shade and therefore lower transpiration demands and increased soil water availability (Holmgren et al. 1997). Thus, species hierarchies and dominance patterns are formed within a plant community and already small changes in temperature and/or precipitation variability might disrupt these existing patterns (Keddy & Shipley 1989; Armas & Pugnaire 2005; Goldstein & Suding 2014). So far, most research of environmental change on plant-plant interactions took place in harsh environments such as deserts, tundra, semi-arid or alpine ecosystems (Tylianakis et al. 2008) resulting in general concepts on how plant-plant

interaction might change with increased water stress under future altered precipitation patterns. These ideas might also apply to mesic temperate grasslands:
Bertness & Callaway (1994) introduced the 'stress-gradient hypothesis': according to this hypothesis, facilitation should be more common when plants are subject to high abiotic stress. There are observations from environments with severe climatic or edaphic conditions which show that neighbouring plants were more facilitative (Maestre et al. 2003; He et al. 2013)**,** but also some studies showed increased competition with elevated stress regimes (Chen et al. 2009; Saccone et al. 2009). Competitive species, as defined by Grime's CSR model of primary plant functional types[2] (Grime et al. 2007), are more susceptible to environmental stress, but are also more readily facilitated than stress-tolerant species: when the current niche of a competitor is expanded by facilitation, the competitive pressure on the stress-tolerant species is increased in return (Chen et al. 2009). However, under extremely severe environmental conditions, only the most stress-tolerant species might persist, because biotic interactions become unimportant relative to the effect of abiotic stress (Michalet et al. 2006).

Drought, heavy rainfall and heatwave: Experimental studies on the effects of single climatic events or altered precipitation variability on plant-plant interactions are rare, especially for mesic temperate grasslands. Saccone et al. (2009) demonstrated that a heatwave in a temperate forest decreased tree seedling survival. They found that the tree canopy could not buffer these negative impacts on the drier (mesoxeric) site as it did on the wetter site (mesohygric). How would the response to the canopy have been on sites with intermediate soil water content? Furthermore, would grass or forb seedlings profit from the canopy of other grass or forb species in the same manner? In an experiment in New Zealand, temperate grassland was treated with extreme heating or heavy rainfall events (White et al. 2001). In this study, the target species were facilitated by the insulating effects of neighbouring plants during the heating event and the rainfall treatment had no effect on the competitive balance of the majority of species. Only some grasses showed reduced competition intensity (White et al. 2001). A review on biotic interactions in the face of climate change (Gellesch et al. 2013) revealed that most studies agree that changes in precipitation and temperature would alter plant-plant interactions, however, there was no general agreement on the effects of climatic drivers on competition. Hence, to get more inside on how plant-plant interactions in mesic temperate grasslands will respond to altered precipitation pattern, this thesis looked at the effects of drought and heavy rainfall events on the interaction among mesic temperate grassland species (**Manuscript 4**), especially on the role of facilitation by legumes under these conditions (**Manuscript 5**).

As mentioned above, ecosystems can be altered by climate variability due to species re-ordering, species extinction, and/or species invasion after the crossing of ecosystem response thresholds (Section 2.2). Furthermore, ecosystems depend on the functionally diverse species composition and the biotic interactions within the ecosystem, if it may be resistant against climatic perturbations and maintain its ecosystem functions. According to Folke et al. (1996) only a limited number of species, so called keystone process species,

[2] C= competitor, S=stress-tolerator, R= ruderal
"The CSR model proposes that the vegetation which develops in a particular place and at a particular time is the result of an equilibrium which is established between the intensities of stress (constraints on production), disturbance (physical damage to the vegetation) and competition (the attempt by neighbours to capture the same unit of resource)." Grime et al. 2007 p.10

drive and control the processes necessary for ecosystem functioning. They form niches in which all other species exist; modifying and maintaining the habitat. The latter group can be seen as the natural insurance capital because their loss, e.g. due to extreme weather events, reduces the plasticity of the ecosystem and its capacity for self-organisation and evolution. Evidence for the application of this theory on grassland was given by Walker et al. (1999). They studied the functional similarity between dominant and minor species, as well as among minor species under changing environmental conditions (here: intensity of grazing). Their results demonstrated that minor species with functions similar to dominant species provided a "reservoir of resilience" due to their ability to increase in abundance under stress. Consequently, alterations in the composition of grassland communities and shifts in existing dominance pattern in the face of increased climate variability might be a hint for the adjustment of the community to climatic perturbation or even an early sign of approaching the threshold to ecosystem state change. Studies on the effects of increased climate variability on the plant species composition of mesic temperate grassland are rare. This might be due to the fact that the grassland community composition in more humid regions is seen to be limited much more by light than by water or nutrients as drought was not a frequent occurrence (Sala et al. 1996). However, due to climate change with increasing frequency and magnitude of drought events this might change. In a recent review on effects of changed precipitation pattern on mesic grassland, a high resilience of grassland systems to altered precipitation amounts and variability on biodiversity was observed (Unger & Jongen 2015). However, the studies with focus on variability are often of short duration and the manipulated variability might still lay in the range of natural inter-annual variability of ecosystems (Unger & Jongen 2015). Thus, if long-term shifts in plant species composition occur in response to altered climate variability, they might not be observed due to the short duration of the experiments (Weltzin et al. 2003).

Drought and heavy rainfall: Engel et al. (2009) found that species diversity, evenness, and richness of a mesic temperate grassland were dominantly influenced by soil moisture. Furthermore, all factors were higher in the dry treatment with 50% reductions of precipitation compared to wet treatment with 50% more precipitation than local average rain amounts. They stated that the response of the dominant species (*Dactylis glomerata, Lespedeza cuneata* and *Trifolium pratense*) to the precipitation treatment probably caused the response of the community as a whole. In the same experimental setup, Kardol et al. (2010) demonstrated that composition and evenness of the subdominant community differed in their response to the precipitation treatment from the response of the grassland community as a whole. This was likely because the dominant species responded directly to the treatment, though the subdominant community might have primarily responded to the changed competitive interactions (Kardol et al. 2010). The importance of both factors, soil water availability and interspecific interactions for regulating the plant community composition was also shown for temperate semi-arid grassland (Yang et al. 2011) emphasizing its generality. Furthermore, in a transplantation experiment a mesic grassland community shifted in its dominance from grasses to forbs due to drier and warmer conditions (Sebastià 2007). According to these findings, shifts in the dominance pattern in mesic temperate grassland can be expected under future drought events which are more frequent, leading to altered ecosystem biomass production and nutrient input as suggested by Kardol et al. (2010).

Inter- and intra-annual precipitation variability: However, how is increased climate variability affecting plant species composition of mesic temperate grassland? In the Buxton Climate Change Impacts Laboratory experiment, grassland composition changed more due to large annual climate fluctuation within 13 years of study than by the applied climate treatments (watering, winter heating, summer drought, and combinations of drought and watering with heating) (Grime et al. 2008). According to Cleland et al. (2013) lower species turnover patterns in response to increased interannual precipitation variability are to be expected in mesic compared to xeric grasslands. They argue that in mesic grasslands, species richness may be buffered due to the dominance of perennial, bud-banking species in mesic systems. In comparison, in xeric systems seed-banking annual species prevail which show higher temporal variability in the appearance and disappearance of rare species sensitive to climate change. Interannual climate variability was also shown to stabilize the long-term coexistence of perennial grass species via variability in competitive interactions enabling species to recover from low densities (Adler et al. 2006). This effect resembled the so called “storage effect” which was previously observed by Chesson & Warner (1981) among coral reef fishes and later discussed in detail by Chesson (2000). It can occur if species have a differential response to their environment, if they are able to buffer their population growth (because they have a long live span such as perennial plants), and if a covariance between environment and competition exists which leads to intraspecific competition concentrated relative to interspecific competition (Chesson 2000).

Temperature variability: Besides interannual precipitation variability, alterations in inter- and intra-annual temperature variability might cause additional stress on grassland plant composition. For example, year-round warming increased forb biomass by 100%, but led to highly variable species richness in a mesic temperate grassland (Hoeppner & Dukes 2012). In the same experiment, the combination of year-round warming and doubled precipitation decreased forb biomass by 53% and species richness declined when warming encountered with 50% less annual precipitation. However, in a French experiment on temperate grassland, year-round warming led to a decline of the fraction of grasses and to an increase of legume fraction in the annual ANPP whereas the forb fraction remained unaffected by warming (Cantarel et al. 2013). Furthermore, seasonality of warming seems to be important as short-term fluctuations in winter temperatures increased freeze-thaw-cycles and induced shifts in species abundance distributions in a mesic temperate grasslands, with grasses benefiting the most (Kreyling et al. 2011).

Interaction of warming and precipitation variability: The interplay between factors such as seasonal or year-round warming and intra-annual precipitation variability may impact vegetation performance. Therefore, **Manuscript 1** focused on this topic. It shows that a more variable precipitation regime with spring or summer droughts coinciding with higher summer temperatures reduced species evenness. However, when a year-round warming treatment coincided with summer drought events, neither the relative abundance of grasses and legumes nor the richness or evenness of the French temperate grassland was affected (Cantarel et al. 2013). It remains unclear if the increased intra-annual climate variability affects plant-plant interaction and community composition of temperate mesic grasslands, or if grassland plant species composition remains resilient against the projected climate change.

2.4 Adaptation and mitigation strategies for mesic temperate grassland to climate change

There are two main response strategies to the projected climate change and to its impacts on grassland: mitigation and adaptation. Mitigation aims to reduce the rate and magnitude of climate change via managing its causal factors such as reduction of greenhouse gas emission or land use change (Washington et al. 2009; IPCC 2012). Mitigation intents to stay clear of critical ecosystem thresholds by reducing the climate-related stress on the system (Lenton et al. 2008; Denton et al. 2014). Adaptation is considered as the process of adjustment (naturally or facilitated by human intervention) to actual climate and its impacts on grassland ecosystems that cannot be avoided (IPCC 2012; Denton et al. 2014). Thus, relevant for climate change adaptation policies might be the question, if qualitative changes of potential tipping elements or even the alteration of ecosystem states can be tolerated (Lenton et al. 2008). Both strategies are needed to reduce the impacts of climate change. However, their combination may lead to conflicting economic and environmental goals (Turner et al. 2010; Denton et al. 2014). The conservation of carbon stocks in grassland soils and the enhancement of atmospheric carbon sequestration is one possible mitigation tool, which could be applied to reduce greenhouse gases. An increase in the carbon sequestration rate in the grassland might be reached for instance via increasing plant diversity (Steinbeiss et al. 2008), higher proportions of legumes (Jensen et al. 2012), fertilizer adjustment (time, amount, formulation) (Soussana et al. 2004; Lal et al. 2011; Schuch et al. 2013; Riggs et al. 2015), irrigation (Olsson et al. 2014), and via biochar or compost amendment (Ryals et al. 2014, 2015; Schimmelpfennig et al. 2014). The change from short-term to permanent grassland can also enhance the C sequestration rate due to decreased nitrate leaching and soil erosion (Freibauer et al. 2004). Furthermore, the reduction of herbivore stocking rates and the extensification of intensive grazing can be beneficial for grassland as carbon sink (Soussana et al. 2004, 2010; Ziter & Macdougall 2013). A study by De Vries et al. (2012) revealed that fungal-based soil food webs and greater microbial evenness in contrast to bacterial-based soil food webs mitigated C and N loss due to drought in extensively managed grassland. However, it is still unclear if global warming will cause C losses from temperate grassland soils due to increased decomposition rates or if the higher decomposition rate is compensated by the higher input of organic material due to higher net primary production stimulated by elevated temperature and atmospheric CO_2 (Parton et al. 1995; Thornley & Cannell 1997; Jones & Donnelly 2004). Increased climate variability in combination with high atmospheric CO_2 concentrations could negatively affect the conservation of grassland carbon stocks and reduces the function of grassland as carbon sinks (Soussana & Lüscher 2007). Ciais et al. (2005) expected that the increased frequency of drought events might turn terrestrial ecosystems from carbon sinks to sources. Whether this is also the case for temperate grassland has yet to be shown.

Assisting mesic temperate grassland to adapt to increased climate variability will often have priority to mitigation strategies because farmers have to maintain forage production and quality in order to keep their incomes and livelihoods (Rosenzweig & Tubiello 2007). Adaptation to increased climate variability might also be different compared to adaptation to changes in mean conditions. Strategies for the latter require more or less adjustment of agronomic techniques, whereas strategies for adapting to increased variability might include avoidance of periods of high stress, increase of resilience, and improvement of soil and water resources (Rosenzweig & Tubiello 2007; Craine et al. 2010; Olesen et al. 2011).

Because the extreme weather events are difficult to predict or control, *'building and maintaining resilience of desired ecosystem states is likely be the most pragmatic and effective way to manage ecosystems in the face of increasing environmental change*' (Scheffer et al. 2001). This goal might be reached via increasing inter- and intraspecific grassland species diversity. Particularly plant species with high genotypic diversity, and thus with a wide range of trait variation, such as differences in root allocation and in tolerance against droughts or pest infestation, can help to increase temperate grassland resistance and resilience against increased climate variability (Beierkuhnlein et al. 2011; Weißhuhn et al. 2011; Poirier et al. 2012; Avolio & Smith 2013). Furthermore, breeding robust plant species varieties with high climate tolerance (Zebisch et al. 2005) or livestock with low nutrient requirements are adaptation strategies for long-term changes (Craine et al. 2010). The creation of new habitats and dispersal corridors in a fragmented landscape can facilitate the conservation and range expansion of specific species (plants, insects, birds) of grassland threatened by climate change (Thuiller 2007; Hodgson et al. 2011). In an alpine grassland experiment, water-saving irrigation measures were used to adapt to changed climate variability. During dry periods they redistributed the water collected during periods with increased precipitation amounts and with water from lakes which have been expanded by the melting of glaciers (Gao et al. 2014). This method doubled grassland productivity and increased plant species richness.

Ecosystems are evolving and their potential futures are often very uncertain and unpredictable. Thus, policies and management actions for adaptation and mitigation have to be flexible and continually modified to the evolving conditions (Holling 1996). Furthermore, the response of ecosystems to all strategies as well as their interactions and consequences have to be properly studied before they are implemented to avoid negative, unwanted effects (Turner et al. 2010). The agronomic techniques of fertilisation and alteration of cutting frequency could have the potential to overcome the influence of climatic conditions in temperate ecosystems (Bradford et al. 2006). However, knowledge of their interactive effects with increased climate variability is lacking. Therefore, **Manuscript 2** and **Manuscript 3** focused on fertilisation and altered cutting regime as possible tools for adapting mesic temperate grassland to increased climate variability. In the following, a short overview about both management types is described in terms of their effects on grassland productivity, forage quality, and plant species composition. Furthermore, already available information on its interaction with climate change is given.

2.4.1 Influence of cutting regime on temperate grassland – frequency and timing

Managed grasslands differ in the cutting regime. Thus, frequency, height, date, and history of cuts vary depending on environmental and economic conditions or on their intended use (forage production, species conservation, recreation). Here, I focus on the effects of cutting time and frequency, as they are two factors I addressed in my manuscripts (**Manuscript 2 & 3**). Especially how the cutting frequency affects productivity of grassland through changes in the morphological development of plants and species composition (Rieder 1983; Pontes et al. 2007). Due to higher cutting frequency, plants remain in the vegetative growing phase where they intensively consume nutrients. Thus, increasing the cutting frequency with simultaneous increases of nutrient application can lead to the full use of the potential yield

(Rieder 1983; Cop et al. 2009). However, cutting grassland more often without raising fertilizer amounts can lead to lower productivity but also to high protein contents in the forage (Wyss 2002). Decreasing the cutting frequency of formerly intensively used grassland can result in lower productivity and higher species richness but also to problems such as pest infestation with e.g. ergot fungus or lower digestibility of the forage (Wyss 2002; Vogel et al. 2012; Kramberger et al. 2014). According to Turner et al. (1993) frequent mowing could limit root growth and the accumulation of belowground N reserves. In terms of forage quality, an increase in cutting frequency can increase the nutritive values of grassland, for instance raising crude protein, nitrogen, and phosphorus content in aboveground plant tissue, decreasing the concentrations of structural carbohydrates, and improving organic matter digestibility (Turner et al. 1993; Cop et al. 2009; Kramberger et al. 2014). Grassland plant species composition can also be affected by cutting frequency (Wyss 2002; Cop et al. 2009). This is due to the differences in the species specific abilities to rapidly reuse stored nutrients and the size of assimilation area of the plant left after the cut (Rieder 1983). Because of the latter, cutting height is also an important factor for grassland growth and plant species composition. A Bavarian grassland vegetation survey showed that species richness was highest in grassland with intermediate cutting frequency, whereas high cutting frequency (≥ 4 cuts per year) and no cutting due to land abandonment had lowest species numbers (Kuhn et al. 2011). Zechmeister et al. (2003) found decreasing numbers of vascular plants in Austrian grassland with increasing number of cuts per year from two to more than three. Furthermore, their results showed that also a minimum cutting frequency was required to maintain species richness. With increasing number of cuts, the use of fertiliser also usually rises. Thus, nitrophilous species are facilitated, which in turn outcompete other species e.g. for light (Plantureux et al. 2005; Diepolder et al. 2006). Besides cutting frequency, cutting time, especially the date of the first cut, is very important for grassland productivity, forage quality, and plant species composition. For successful grassland management the cutting time has to be a good compromise between dates where yield is high, but where also high forage quality is obtained. This is because the latter is decreasing with maturity (Hopkins & Wilkins 2006; see section 2.3.2). Furthermore, an early first cut affects the number of grass shoots of the second growth. This is because cutting the mature shoots stops their inhibition on the lateral shoots, and thus, their growth is facilitated (Rieder 1983). The timing of cuts is also influential if grassland species are able to flower and produce mature seeds. In extensive grassland, e.g. hay meadows, an early cut (e.g. in May) and a late cut (e.g. in September) could permit a delay in flowering and enable mature seed production (Plantureux et al. 2005). Whereas in more intensively used grassland late cuts might lead to stimulation of forb species or even overspreading of unfavourable forbs (Kramberger & Kaligaric 2008).

In **Manuscript 2**, the variation of the cutting date was tested in combination with and without fertilization on their ability to adapt grassland to increased precipitation variability. Studies on interactive effects of cutting regimes and climate changes are rare. Frequent cutting homogenizes plant species' growth patterns and changes species composition. Therefore, the cutting regime might disrupt the correlation of grassland productivity and precipitation amount (Swemmer & Knapp 2008). This agrees with findings of Bernhardt-Romermann et al. (2011), where intermediate cutting frequency together with fertilisation reduced the effects of climatic variability on grassland yield compared to impacts of biodiversity. However, **Manuscript 3** revealed that increased cutting frequency (4 vs. 2 cuts per year) in extensively used grassland neither buffered, nor amplified the adverse effects of precipitation variability on productivity. In contrast, Kramberger et al. (2014) found a high correlation of annual grassland production with a precipitation amount for more frequently cut grassland (≥ 3 cuts

per year) compared to the treatment with two cuts per year. Thus, longer dry periods affected grassland with higher cutting frequency more. Comparably, reduced resistance of grassland biomass against drought was shown for frequently (4 cuts per year) cut grassland compared to grassland which was cut less frequently (Vogel et al. 2012).

2.4.2 Influence of fertilisation on temperate grassland

Besides optimal site and management conditions, a good nutrient supply is needed for high growth rates of grassland species (Nösberger & Opitz von Boberfeld 1986). In general, nitrogen is the most limiting nutrient in forage production because of a complex nitrogen balance and extremely dynamic soil N status (Voigtländer & Jacob 1987; Barker & Collins 2003). Plant growth uses large amounts of soil nitrogen, but plant-absorbable forms of N are highly soluble and thus subjected to leaching. Furthermore, the provision of N from soils depends on e.g. N fixation by legumes, N mineralization rates and atmospheric depositions (Voigtländer & Jacob 1987; Barker & Collins 2003). When N fertiliser is applied, other nutrient concentrations such as of phosphorous (P) and potassium (K) in soil have to be controlled to prevent productivity or quality restrictions (Voigtländer & Jacob 1987). P fertilisation can facilitate legumes if sufficient K is present, and due to the N fixation by legumes, P fertilisation alone can increase grassland productivity. Beside N, P and K, the synergistic co-limitation of micronutrients such as iron, manganese, boron or copper can also be decisive for grassland productivity (Fay et al. 2015). Extensively used grassland (1-2 cuts per year), which is poor in legumes, needs fertilisation to be productive except when it is grown on organic, N rich soils. In climatic favourable regions and on mineral soils, fertilisation increases the species growth rate of extensively used grassland which then has to be cut more often to harvest qualitatively good forage (Voigtländer & Jacob 1987). Furthermore, if legume content is high on these sites (>30%), N fertilisation is not rewarding in terms of productivity (except when an intensification is pursued), though P and K fertiliser might stabilize the sward (Voigtländer & Jacob 1987; Barker & Collins 2003). Fertilisation of intensively used grassland (≥3 cuts per year) is needed due to enhanced N uptake for shooting and leaf growth (Rieder 1983). In these systems, fertilisation is most effective were soil N content and N amounts fixated by legumes is low (Voigtländer & Jacob 1987). Therefore, fertilisation usually increases grassland productivity in managed grassland (Wyss 2002; Barker & Collins 2003; Cop et al. 2009). Additionally, an optimal nutrient supply is important for a good forage quality. Higher nitrogen supply is visible in the increase of nitrogenous compounds and structure of plants (Nösberger & Opitz von Boberfeld 1986). Particularly crude protein content rises with nitrogen fertilisation (Collins & Fritz 2003; Balabanli et al. 2010). Furthermore, fibre, cellulose, and lignin content were found to decrease after N fertiliser application (Balabanli et al. 2010). Wyss (2002) found that doubling the fertilizer amount but keeping cutting frequency constant led to slightly higher energy and protein content in forage. However, if some element concentrations such as potassium are too high, the availability for other elements (e.g. magnesium) may be decreased (Voigtländer & Jacob 1987; Ball et al. 2001). Fertilisation can also affect grassland species composition (Wyss 2002). N application is facilitating especially for competitive and/or nitrophilous species (such as tall grass species) whereas other species are suppressed (Voigtländer & Jacob 1987; Schellberg et al. 1999; Plantureux et al. 2005; Cop et al. 2009). Plantureux et al. (2005) mentioned observations where species number were reduced by 50% after

application of 20-50 kg N ha^{-1} $year^{-1}$. This agrees with Zechmeister et al. (2003) who showed that total plant species richness decreased with increasing nitrogen supply. However, depending on the site and management conditions (see 2.4.1) species will respond differently to fertilization (Schellberg et al. 1999). If nutrient supply is insufficient, productivity of several grassland species will adjust over time resulting in species rich grassland communities because competition for light is less strong (Nösberger & Opitz von Boberfeld 1986; Suding et al. 2005). A lot of these species would be otherwise suppressed on a fertilized and therefore highly productive grassland (Voigtländer & Jacob 1987).

There are only few studies looking at the interactive effects of fertilisation and climate change on grassland, although a better understanding of these complex interrelationships with diversity, productivity and stability is required for sustainable grassland management in the face of climate change (Hautier et al. 2014). The existing studies mainly focussed on drought: During drought N uptake by plants is reduced (Durand et al. 2010), though a fast recovery of nutrient uptake rate and a higher growth rate of fertilised grassland should lead to faster regrowth after drought events (Lee & Rudge 1986). Hartmann & Niklaus (2012) did not find evidence for compensatory growth after drought on grassland with or without higher N supply. However, long-term studies showed that in fertilised grassland the long-term annual yield was not affected, or less decreased, by altered precipitation distribution with longer periods of low precipitation compared to unfertilised grassland (Swemmer et al. 2007; Kramberger et al. 2014). In addition, Klumpp et al. (2010) found that precipitation quantity and seasonal distribution was important for the carbon storage of moderately intensive managed grassland with N supply which increased during drought. Furthermore, a positive relationship of resilience to drought and species richness was found only in frequently mown (4x) and high fertilised treatment due to alterations of the shoot-root ratio (Vogel et al. 2012).

Thus, fertilisation can positively affect grassland yield, quality, and composition. The studies mentioned above indicate that higher N supply might also be beneficial in the face of drought events. Because it is an agronomic technique, which is fast and easily applicable, its potential to overcome the influence of altered intra-annual climate variability was studied in **Manuscript 2.**

2.5 Challenges and limitations of climate change experiments – bridging the gap between experiments and models

Plant responses to changing mean climate can be studied well by long-term observations, but observational studies are seen to be less suitable to study plant responses to climate variability and its underlying processes (Reyer et al. 2013). This is due to the fact that many factors are involved which are usually not measured. In contrast, experiments in the field or in the laboratory can incorporate climatic variability, especially the occurrence of extreme climatic events or a seasonal difference in climate e.g. warmer winters but cooler springs (Reyer et al. 2013; Thompson et al. 2013). In particular, in field experiments, processes and impacts of climate change can be studied in the most natural conditions as possible including ecosystem complexity (Kreyling et al. 2014). Furthermore, they are suitable to elucidate cause-and-effect relationships and to gain a mechanistic understanding of short-term ecosystem response to single or multiple drivers of climate change (Rustad 2006, 2008).

The need to include climate variability in climate change experiments is recognized (Jentsch et al. 2007; Thompson et al. 2013; Kreyling et al. 2014). Yet, several studies failed to properly incorporate climatic variability in particular seasonal variation and extremes in temperature (Thompson et al. 2013; Kreyling & Beier 2013). Advances in experimental infrastructure are stipulated that allow realistic manipulations of climatic extremes without potentially confounding artefacts (Smith 2011). Possible artefacts and several dilemmas associated with the design of precipitation change experiments and applied manipulation treatments were recently reviewed by Beier et al. (2012). For instance, they pointed out that treatment strength which exceeds thresholds and other disturbing factors (e.g. fire, herbivory) are deliberately avoided to not impair the original experimental set-up. Nevertheless, these factors could naturally lead to important interactions with projected precipitation change. Excluding natural disturbance or disregarding the successional state of the ecosystems recovering from disturbance can lead to the underestimation of the impacts of climate change (Kröel-Dulay et al. 2015). Furthermore, the climate scenarios applied in experiments are often not as complex as projected because it would be otherwise a huge economical and practical effort and difficult to disentangle the cause of observed changes (Beier et al. 2012).

Although, testing for example multiple climatic and non-climatic drivers and their combined effects on ecosystems is important because single factor studies were shown to overestimate ecosystem responses (Leuzinger et al. 2011a; Larsen et al. 2011). Thus, multifactor experiments are needed to reveal interactions among climatic and non-climatic drivers and to receive realistic ecosystem responses (Larsen et al. 2011; Kreyling & Beier 2013). Economic constraints also prohibit sufficient spatial extension and duration of the experiment to provide relevant information on long-term effects (Beier et al. 2012). Besides these dilemmas, Beier et al. (2012) summed up examples for water related, physical, or microclimatic artefacts which have to be considered such as uneven water distribution, lateral water inputs, plant death as well as shading or passive warming by rain-out shelters. In addition to precipitation manipulation artefacts, a comparison of warming techniques in climate research highlighted the influence and complexity of warming simulation on plant performance (Backhaus et al. 2014b). Co-varying parameters, such as evapotranspiration, photosynthetically active radiation, and wind speed have to be closely surveyed and considered when analysing the response of plants to the applied climatic treatment (Backhaus et al. 2014b). Furthermore, Beier et al. (2012) showed that the available

precipitation manipulation experiments are differing in several aspects e.g. representation of climatic and ecosystem characteristics, experimental design, and species and genotype diversity. These differences make comparisons and meta-analyses difficult. Beier et al. (2012) recommend several aspects to be considered in future experiments that would improve the understanding of climate change effect on ecosystems. In this context, Vicca et al. (2012) demands a common denominator to characterize actual precipitation treatments to compare ecosystem responses to changes in water availability across experiments. For example, Fay et al. (2011) used the coefficient of variation (CV) for quantifying the intra-annual precipitation variability in their experiment. Thus, CV was included in the work at hand (**Manuscript 1-3**) to characterize the precipitation variability treatment and for better comparison of results.

Another challenge for climate change experiments is the choice of a suitable climate scenario because climate model projections have general uncertainties and have regional differences (Beier et al. 2012; Thompson et al. 2013; Kreyling & Beier 2013). Thompson et al. (2013) therefore suggest that the design of climate change experiments should include climate variability as an ensemble of ecological treatments and not just a single realisation.

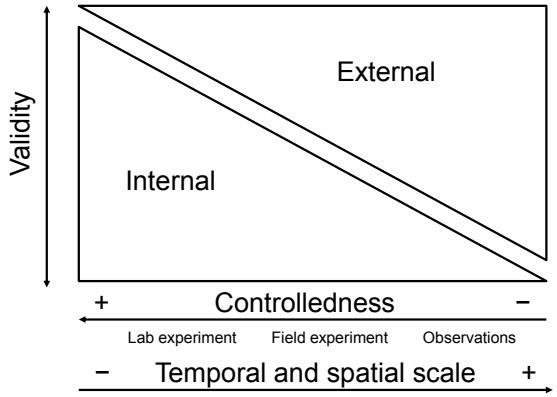

Figure 6 A schematic representation of the trade-off between internal validity (being able to attribute a change to a specific factor) and external validity (the confidence with which results can be generalized) (figure and caption according to De Boeck et al. (2015))

Recently, De Boeck et al. (2015) also addressed some of these challenges that experimentalists are confronted with and discussed on how they can significantly affect the extrapolation of findings. They highlighted the trade-off between the external and internal validity which results from the variation in the degree of controlledness and of the temporal and spatial scales between experiments in the laboratory, field experiments, and observations (Figure 6). According to De Boeck et al. (2015), a higher degree of control on smaller scales enables the attribution of a change to a specific factor (internal validity). Simultaneously, the confidence for the generalisation of the results is reduced (external validity). In turn, less control and higher temporal and spatial scales (e.g. in observations) allows a better representation of natural complexity. The generalisation of results thereby can be more straightforward, although underlying mechanisms are less understood. For appropriate extrapolation of findings, it is important to recognize the position of a study on this internal-to-external-validity gradient and to consider its limitations (De Boeck et al. 2015, Figure 6).

Therefore, Kreyling & Beier (2013) and De Boeck et al. (2015) recommend regression or gradient experiments that focus initially on understanding the process by running single climate factor experiments including their variation in intensity and frequency. These experiments should be followed by coordinated experiments distributed over multiple sites (such as descripted in Fraser et al. (2013) and applied in Fraser et al. (2015)) for generalisation of their findings. In the next step, process-based modelling should lead to virtual experiments with combinations of drivers whose findings than could be verified by more complex multifactor experiments (Kreyling & Beier 2013). This agrees with Reyer et al. (2013) and Kreyling et al. (2014) who see models crucial to capturing plant responses to changing climatic variability and therefore should be used in combination with experimental and observational studies to overcome the limitations of individual approaches and up-scaling problems. Models are helpful tools as they allow testing of concepts and understanding of processes by integrating existing knowledge (Rustad 2008; De Boeck et al. 2015). Additionally, models can complement empirical research and project experimental results in time and space (Rustad 2008; Lee & Mishurov 2013). However, similar to experiments, models need yet to improve the integration of the variability of climate factors as well as biodiversity and disturbance (Classen & Langley 2005; Rustad 2008). Although the need to combine climate experiments and models is acknowledged, experimental data is not often useful for modelling e.g. due to site-level idiosyncrasies and shortcomings of single experiments, the lack of relevant synthesis metrics, or unavailability of access to experimental data (Dukes et al. 2014; De Boeck et al. 2015). Thus, **Manuscript 6** compares processes measured in precipitation manipulation experiments and how they are implemented in land surface models. It gives recommendations how data from field experiments could be better integrated into models in order to improve the connectivity between precipitation manipulation experiments and models.

3 Summary of manuscripts presented in this thesis and declaration of personal contribution

The following section gives a short summary of the manuscripts forming this thesis with focus on the most important findings of each study including the declaration of personal contribution to each manuscript. The field work for Manuscripts 1 – 3 was carried out in the multifactorial EVENT-2 experiment designed to test the response of semi-natural, mesic temperate grassland to manipulated alterations in intra-annual precipitation variability (low, medium, 2 x high: with spring or summer drought events), management practices (cutting regime, fertilisation) and seasonal warming (winter, summer). The field work for Manuscript 4 and 5 took place in the two-factorial EVENT-1 experiment testing the response of artificial grassland communities to the manipulation of extreme weather events (drought and heavy rainfall) and community composition. For more details on the experiments please refer to the methods sections in the manuscripts. Manuscript 6 is a review which grew out of an organized oral session on precipitation manipulation experiments at the 96th Annual Meeting of the Ecological Society of America.

Manuscript 1

Title: Importance of seasonality for the response of a mesic temperate grassland to precipitation variability and warming
Authors: **Kerstin Grant**, Jürgen Kreyling, Carl Beierkuhnlein, Anke Jentsch
Journal: Ecosystems, submitted 02.12.2015
Personal contribution: data collection: 30%, data analysis: 90%, writing: 90%, concept: 80%, discussion and editing: 80%, corresponding author

Manuscript 1 presented that the seasonal occurrence of the climatic factors, here early vs. late drought events in the high intra-annual precipitation variability treatments, seemed to be an important driver of the shifts in community composition but not for decreases in aboveground net primary productivity (ANPP) compared to regular rainfall pattern throughout the entire growing season. Only the treatment with a high precipitation variability including spring drought events favoured forbs over grasses. Furthermore, the timing of chronic warming, here winter vs. summer, altered the direction of response of both, community composition and ANPP. Winter warming increased ANPP and favoured forbs while summer warming showed no significant effect on biomass but decreased species richness. The interaction of the precipitation and temperature variability treatments showed an interesting response: a more variable precipitation regime with spring or summer droughts coinciding with higher summer temperatures reduced species evenness and likely promoted the establishment of specialists and drought tolerant species. Because ecological effects and processes to the timing of climate factors might be divergent or hidden if not separately studied, future climate change experiments should include the seasonality and timing of climatic factors depending on the local climate projections.

Manuscript 2

Title: Water stress due to increased intra-annual precipitation variability reduced forage yield but raised forage quality of a temperate grassland

Authors: **Kerstin Grant**, Jürgen Kreyling, Laura F.H. Dienstbach, Carl Beierkuhnlein, Anke Jentsch

Journal: Agriculture, Ecosystems & Environment 186 (2014) 11–22

Personal contribution: data collection: 40%, data analysis: 90%, writing: 90%, concept: 70%, discussion and editing: 80%, corresponding author

Manuscript 2 focused on how water stress due to increased intra-annual precipitation variability reduced forage yield (ANPP) but raised forage quality of mesic temperate grassland. It further presented how two land management strategies namely fertilization and alteration of harvest date (delay by 10 days) interact with altered precipitation regime. In agreement with Manuscript 1, this study showed that community composition was altered due to increased intra-annual precipitation regimes with spring drought events in terms of less biomass of grasses and more forbs. Fertilization during drought periods and harvest delay after drought periods were only partially successful as management strategies to sustain forage production under more extreme precipitation regimes. They proved to be less effective if the extreme weather event occurred later in the season. A nitrogen dilution effect (decreased plant nitrogen concentration with increasing shoot biomass) might have masked possible effects of precipitation variability on plant nitrogen and therefore on quality of grassland species. However, the results of this study emphasized the importance of seasonality in climatic factors for the responsiveness of grassland performance as changes in community composition and plant senescence were main drivers of forage quality response to changed precipitation patterns.

Manuscript 3

Title: Increased rainfall variability reduces biomass and forage quality of temperate grassland largely independent of mowing frequency

Authors: Julia Walter, **Kerstin Grant**, Carl Beierkuhnlein, Juergen Kreyling, Michael Weber, Anke Jentsch

Journal: Agriculture, Ecosystems & Environment 148 (2012) 1–10

Personal contribution: data collection: 30%, data analysis: 30%, writing: 10%, concept: 30%, discussion and editing: 50%

Manuscript 3 addressed a possible interaction between the land management practice cutting frequency and intra-annual precipitation variability on productivity and forage quality. Increased precipitation variability caused a reduction of ANPP of temperate grassland and short-term decreases in forage quality, in terms of lower leaf N and protein concentrations. An increase in cutting frequency (4 vs. 2 times a year) enhanced the root-shoot ratio and the concentration of leaf N. However, more frequent cutting neither buffered, nor amplified the adverse effects of higher precipitation variability on productivity, but caused a reduction in leaf N concentrations in early summer. This study also included a comparison of the response of ANPP to the alteration of changed inter- and intra-annual precipitation variability (first year of the study) vs. intra-annual precipitation variability with constant annual

precipitation amount (second year). There was evidence that the combined changes in the amount, timing and frequency of precipitation enhanced plant water stress and can lead to higher impacts on agricultural yields.

Manuscript 4

Title: Extreme weather events and plant-plant interactions – Shifts between competition and facilitation among grassland species in the face of drought and heavy rainfall
Authors: **Kerstin Grant**, Jürgen Kreyling, Hermann Heilmeier, Carl Beierkuhnlein, Anke Jentsch
Journal: Ecological Research (2014) 29: 991–1001
Personal contribution: data collection: 75%, data analysis: 95%, writing: 90%, concept: 95%, discussion and editing: 80%, corresponding author

Manuscript 1 and 2 revealed changes in the community composition of grassland due to increased intra-annual rainfall variability and indicated that plant-plant interactions might have influenced the response of grassland to extreme weather events. Thus, Manuscript 4 looked at plant-plant interactions, namely facilitation and competition, between temperate grassland species in the face of extreme drought and rainfall events as part of altered rainfall variability. Species specific shifts in plant–plant interactions from facilitation to competition or vice versa were caused by single climatic extremes. The study revealed that the nature of the shifts varied depending on the particular community composition. Because drought did not affect ANPP of this experimental grassland community, the complementary response in competition intensity – shift from competition to facilitation for *Arrhenatherum elatius* and a contrasting shift for *Lotus corniculatus* – might indicate that changes in biotic interactions as one of the mechanisms for stable community productivity in the face of drought. Furthermore, the results on plant-plant interactions suggested that the presence of a legume in the plant communities appeared to have a key role in the response of competition intensity experienced by grasses to climate change.

Manuscript 5

Title: Climatic extremes lead to species-specific legume facilitation in an experimental temperate grassland
Authors: Mohammed Abu Sayed Arfin Khan, **Kerstin Grant,** Carl Beierkuhnlein, Jürgen Kreyling, Anke Jentsch
Journal: Plant and Soil (2014) 379:161–175
Personal contribution: data collection: 25%, data analysis: 5%, writing: 5%, concept: 10%, discussion and editing: 20%

Manuscript 5 addressed the role of nitrogen-fixing legumes, here *Lotus corniculatus*, in the response of grassland productivity to four years of yearly recurrent drought and heavy rainfall events. Aboveground net primary productivity of neighbouring non-legumes was facilitated by legumes under ambient weather conditions and when the experimental grassland communities were exposed to heavy rainfall events. However, this facilitative legume effects

on neighbouring plant growth disappeared under extreme drought. Species identity was decisive for the response to legume effect on productivity but also on δ15N, leaf N concentration and N uptake. We argued that the missing legume effect on community productivity under drought was caused by reduced N-uptake of target species rather than reduced N-fixation by the legume. The findings emphasised the importance of legume presence for stabilizing grassland performance under future increased precipitation variability.

Manuscript 6

Title: Toward a better integration of biological data from precipitation manipulation experiments into earth system models

Authors: Nicholas G. Smith, Vikki L. Rodgers, Edward R. Brzostek, Andrew Kulmatiski, Meghan L. Avolio, David L. Hoover, Sally E. Koerner, **Kerstin Grant**, Anke Jentsch, Simone Fatichi, and Dev Niyogi

Journal: Reviews of Geophysics (2014) 52(3):412–434

Personal contribution: literature research 5%, writing: 0%, concept: 0%, discussion and editing: 5%

Manuscript 6 aimed to bridge the gap between precipitation manipulation experiments and Earth system models. It gave recommendation on how biological data from field experiments could be better integrated into models and should reignite the necessary dialog between the different research communities. The manuscript reviewed most recent projections for future terrestrial presentation, the structure and functioning of the current-generation of land surface models (LSM) and different approaches of precipitation change field experiments. It further pointed out routine measurements (e.g. soil moisture and micrometeorological data in high temporal and spatial resolution, soil water retention curves, respiration rates, plant functional types etc.) that would improve the incorporation of useful data and more refined processes into models. We further compared biological processes commonly measured in the field, namely carbon assimilation and productivity, phenology, soil organic matter decomposition and plan community dynamics with their model analogs. We found that often the measured processes are not compatible with the way they are represented in LSMs. Additionally we addressed the challenge of scaling from plot to globe. In conclusion, the global change community would benefit most from experiments designed by researchers of both communities – field ecologists and modelers.

4 Main findings of the thesis

In this section the main findings identified in my research are presented and organized to answer the research questions.

How does increased intra-annual precipitation variability affect the annual net primary productivity of mesic temperate grassland?

The findings of this thesis showed that aboveground biomass of the grassland communities was not altered by a single extreme drought or heavy rainfall events, although soil moisture was significantly reduced and increased, respectively, implying high plant water stress (**Manuscript 4**). Effects of extreme weather events on grassland productivity were only found on plant level where the plant biomass response was species specific and dependent on the community composition (**Manuscript 4**). Other experimental studies confirmed that plant communities facing single or annual recurrent extreme weather events are more stable than previously thought (Jentsch et al. 2011; Backhaus et al. 2014a). However, an increase in intra-annual precipitation variability, as projected for the future (see Section 2.1.2), will result in longer dry periods followed by intense rain events and therefore to an accumulation of different kinds of plant water stress (e.g. low soil moisture content, water-logging; Section 2.2). The manipulated increase of precipitation variability in this thesis resulted in higher soil moisture variability and likely in high plant water stress (**Manuscript 1 & 3**). In the high intra-annual precipitation variability treatment, mesic temperate grassland was exposed to annually recurrent 1000-year drought events (in late spring and summer, respectively) always followed by a heavy rainfall event. Over the five-year study period, high intra-annual precipitation variability decreased aboveground net primary productivity of the grassland by about 19% compared to a low variable treatment characterized by continuous water supply without major drought stress (**Manuscript 1, 2 & 3**). Furthermore, it changed the functional group biomass. High precipitation variability with spring drought events favoured forbs over grasses (**Manuscript 1**). In general, ANPP did not decrease gradually along the precipitation variability manipulation of low to medium to high levels: ANPP of the medium precipitation variability treatment (characterized by ambient precipitation with four larger rainfall events) resembled the ANPP of high precipitation variability treatments (**Manuscript 1**). **Manuscript 3** revealed that the effects of high intra-annual variation in precipitation on ANPP were stronger in years with low precipitation amounts indicating that the overall rainfall amount was more important for temperate grassland productivity. Thus, intra-annual precipitation variability was correlated with interannual changes in precipitation amounts: alterations in intra-annual precipitation variability, that accompanied changes in total precipitation amount, amplified the effects on temperate grassland productivity. Therefore, the increase of both, inter- and intra-annual precipitation variability, seemed to be a threat for grassland performance. Moreover, **Manuscript 1** revealed that the seasonality of climatic factors, here early (May-June) versus late (July-August) drought events in the high precipitation variability treatments, was not important for the decrease in ANPP. Both high precipitation variability treatments decreased ANPP compared to low precipitation variability.

For understanding possible processes behind the impacts of increased intra-annual precipitation variability on plant productivity, belowground processes should not be neglected. Although the main focus of this thesis was on aboveground changes, the thesis revealed that increased intra-annual precipitation variability had no long-term effects on

belowground net primary productivity here assessed in terms of root length (**Manuscript 2**). A short-term effect of altered rainfall variability on root length occurred in one study year (**Manuscript 3**): root length in July 2009 was lower in the face of both, high and low precipitation variability, compared to medium precipitation variability. Besides a reduction of root growth following directly after extreme drought and rainfall events in the high variability treatment, regular water availability was found to reduce the stimulation of root growth. This confirms that increased belowground resources usually favour shoot over root allocation (Field et al. 1992). Furthermore, under low precipitation variability it was not necessary to increase the proportion of water-absorbing biomass to exploit limiting water resources (Kalapos et al. 1996). However, this kind of enhanced root growth as an adaptive response to reduced water resources partly explains the increased root length and lasting reduction of root-to-shoot ratio under medium precipitation variability. Thus, drought adaptive root growth can only be expected for short and intermediate drought events but not for high precipitation variability with longer drought events.

What are the consequences of increased intra-annual precipitation variability on forage quality?

In this thesis, the influence of increased intra-annual precipitation variability on the quality of grassland forage was tested, because more extreme precipitation regimes seem to have the ability to change plant physiological processes and nutrient availability (Jentsch et al. 2011) which could lead to reduce forage quality. **Manuscript 3** showed that increased intra-annual precipitation variability decreased the leaf nitrogen concentration and leaf protein content of two temperate grassland species (*Alopecurus pratensis, Trifolium pratense*) indicating reduced forage quality. However, analyses of mixed samples of all grassland species (following an agriculture routine for forage quality assessment) revealed that increased intra-annual precipitation variability increased the crude protein content and metabolisable energy for cattle and pig (**Manuscript 2**). Furthermore, it decreased the fibre content of temperate grassland. On the one hand, these contrasting results showed the influence of the chosen sampling methods and indicated misinterpretations that could arise when scaling up experimental results from single plant level. On the other hand, the results showed that increased intra-annual precipitation variability was affecting plant performance species specifically leading to reduced forage quality on plant level, though the forage quality of the whole grassland community was increased by high precipitation variability. In addition, the thesis revealed that the main driver for forage quality change was the alteration in the plant community composition with varying precipitation regime. Evidence for this was given by the different pattern in nutrient content change among the single species (**Manuscript 3**) and changed functional group biomass (**Manuscript 1**) along the precipitation variability gradient. Additionally, legumes were shown to alter plant nitrogen uptake of neighbouring non-legume species (**Manuscript 5**). Legumes biomass was changed with precipitation variability and was highest under medium precipitation variability (**Manuscript 2**), thus, probably contributing to the alterations in forage quality. Moreover, plant maturity stage and senescence, altered by the plant water stress, could be seen as a further driver of this change in forage quality. Taking into account a possible nitrogen dilution effect – decreased plant nitrogen with increasing plant mass (Lemaire & Gastal 1997) – the observed increase of forage quality due to increased precipitation variability might have been impaired because biomass production was simultaneously decreased (**Manuscript 2**).

Is plant community composition changing due to increased intra-annual precipitation variability?

Increased intra-annual precipitation variability shifted the plant community composition of temperate grassland in terms of alterations in species evenness and changes in the biomass and evenness of functional groups (**Manuscript 1 & 2**). Species richness was not affected by increased precipitation variability. High precipitation variability with a spring drought event led to an increase of forb and decreases of grass biomass in comparison to regular water availability. Legume biomass was decreased by high precipitation variability with both, early and late drought events, compared to a moderate variable precipitation regime. This varying behaviour of plant functional types in response to altered precipitation patterns was likely caused by different plant adaptation strategies and growth forms, such as rhizomatous structure, leaf structure, and bud position, as well as timing differences of phenological stages (Sternberg et al. 1999; Kammer 2002). With the decrease of the dominant grasses and an increase of forbs but unchanged species richness, the functional groups became more evenly distributed within the community. If this higher evenness also includes high trait variances, which was not studied here, the grassland community should have a better adaptive capacity and should sustain long-term productivity when precipitation variability continues to increase (see Section 2.2 and Norberg et al. 2001; Hillebrand et al. 2008). However, species evenness was decreased by high precipitation variability with late summer drought events. This lower species evenness might have decreased the temporal stability of the community and probably caused the observed decrease in productivity via affecting grassland functions e.g. water retention. Furthermore, the thesis showed that seasonality of climatic factors, here early vs. late drought events in the high precipitation variability treatments, was important in driving the shifts in community composition.

Interaction of multiple climate factors: Are effects of increased precipitation variability on the productivity and community composition of temperate grassland amplified when it is co-occurring with seasonal warming?

Multifactor experiments are necessary to reveal interactions among climatic and non-climatic drivers and to receive realistic ecosystem responses (Larsen et al. 2011; Kreyling & Beier 2013). So far, more complex changes in temperature and precipitation variability are not yet well covered. This thesis showed that the timing of seasonal warming, here winter vs. summer, affected the direction of response of both, ANPP and community composition. Winter warming increased ANPP by 12% while summer warming showed no significant effect on biomass but decreased species richness. Remarkably, the effects of altered precipitation variability and warming on ANPP were independent from each other. These additive results of grassland productivity are contrary to the findings of other multifactor climate change experiments. For example, Hoeppner & Dukes (2012) showed that mesic grassland productivity remained stable across single factor manipulations but that drought limited the capacity of the grassland system to withstand warming by suppressing total and shoot production. **Manuscript 1** revealed that changes in seasonal temperature and intra-annual precipitation variability can alter the functional composition of temperate grassland. Both, winter warming and high precipitation variability with spring drought events, favoured forbs over grasses. Furthermore, species evenness was decreased when summer warming coincided with increased precipitation variability. Less variable precipitation regimes during

warmer summers favoured an even distribution of species. However, a higher variance in species under summer warming and extreme precipitation variability probably promoted the establishment of specialized plant species which tolerate extreme events and quickly adapt to variable precipitation patterns. According to the findings of **Manuscript 1**, the expected changes in temperature and intra-annual precipitation regimes will not amplify the effects on the productivity of mesic temperate grassland. However, the opposite shifts in grassland functional composition to summer and winter warming emphasize the ecological importance of the seasonality of climate warming. The novel aspect, testing seasonal and not all-year round warming, revealed divergent response in plant performance. Thus, climate change experiments should not only test for the interaction of multiple factors but should also recognize the seasonality and timing of climatic factors depending on the projections of their study. Neglecting the timing of climatic factors might hide underlying processes, which are important to reveal for understanding and mitigating climate change.

Investigating underlying processes that alter the resistance and resilience of temperate grassland: What role do plant-plant interactions play for grassland productivity in the face of increased precipitation variability?

Understanding processes like competitive dynamics under fluctuating resources is important for assessing plant community shifts and degree of stability of ecosystem functions. One of the 100 fundamental questions Sutherland et al. (2013) identified is “Which factors and mechanisms determine the resilience of ecosystems to external perturbations (…) ?”. This thesis revealed that plant-plant interactions, here competition and facilitation, were affected by increased precipitation variability (**Manuscript 1 & 4**). **Manuscript 4** showed that the competitive behaviour of grassland species is species specific and sometimes reciprocal under the influence of extreme weather events. Already single climatic extremes caused shifts in plant-plant interactions from facilitation to competition or vice versa, but the nature of the shifts varied depending on the community composition. The complementary responses in competition intensity experienced by grassland species under drought suggest plant-plant interactions as one stabilizing mechanism for overall community performance, because ANPP of the plant community was not affected by the drought. Additionally, species evenness was found to decrease by high precipitation variability with late summer drought events, while functional group evenness remained unchanged indicating the facilitation of, or competition on, single species by precipitation though not on certain functional groups (**Manuscript 1**). Increased intra-annual precipitation variability can have indirect consequences on ecosystem processes via altered plant-plant interactions and dominance shifts in the community composition. For example, the observed shift in community composition by the altered precipitation pattern was found to be the main driver of changes in forage quality (**Manuscript 2**). In addition, this thesis revealed that the presence of a legume in a grassland community has a key role in the response of competition intensity experienced by grasses to increased precipitation variability (**Manuscript 4**). Moreover, legumes facilitated the productivity of neighbouring plant species via their ability of fixing additional atmospheric nitrogen, transferring it to neighbouring plants via root exudation and reducing the competition for soil nitrogen (**Manuscript 5**). This facilitative legume effect was not affected by heavy rainfall events. However, the positive legume effects on growth disappeared under extreme drought conditions (**Manuscript 5**). Thus, these findings additionally emphasize the importance of functional diversity and species-specific traits

additional to the complementarity of species competitive response for maintaining a stable productivity in the face of increased intra-annual precipitation variability.

Finding adaptation strategies: Does fertilisation and varying cutting dates, or the alteration of cutting frequency, buffer negative effects of increased intra-annual precipitation variability on productivity and forage quality of temperate grassland?

The dimension of the impact of increased climate variability on grassland systems is not completely foreseeable yet. Therefore, adaptation strategies have to be identified as soon as possible to counter negative effects on grassland. In this thesis, agronomic techniques, which are fast and easily applicable, namely fertilisation and alteration of cutting regime, were tested for their suitability as adaptation tools to overcome the influence of altered intra-annual climate variability on mesic temperate grassland. To my knowledge, this was the first approach specifically targeting adaptation of grassland to increased intra-annual precipitation variability. Fertilisation was shown before to positively affect grassland productivity, quality, and composition (Section 2.4.2). However, **Manuscript 2** revealed that fertilization during drought periods and a 10-day harvest delay after drought periods – allowing for plant recovery before harvest – were only partially successful as management strategies to sustain grassland biomass production and forage quality under more extreme precipitation regimes. Although key nutritive values, e.g. crude protein, were increased due to the application of fertilizer, fertilisation had no influence in maintaining forage quality under high intra-annual precipitation variability. Furthermore, fertilisation during a drought period did not alter the direction of response of grassland biomass production to extreme precipitation variability. Nonetheless, losses in grassland annual biomass productions, which were induced by extreme precipitation variability, were reduced by fertilisation. A 10-day delayed grassland harvest after drought was applied to enable fertilizer to increase soil nutrient availability and encourage fast recovery of plants. This method proved not to be an effective management strategy in the face of varied precipitation patterns. Although it increased total and grass biomass, the harvest delay decreased crude protein content mainly due to the additional time for plant growth and further lignification of plant material. However, the decrease in forage quality by the delayed harvest was outweighed by the increase in forage quality as a consequence of modified intra-annual precipitation variability. The timing of extreme weather events was a determining factor in the responsiveness of forage quality to the tested management strategies, here expressed as varying response in the crude protein content and gas production. They proved to be less effective at the precipitation variability treatment where drought and heavy rainfall events occurred later in the season compared to the treatment with extreme weather events earlier in the season. The advanced maturity of plants later in the season, causing lower leaf/stem ratio and higher fibre content due to further lignification of plant tissue, was mainly responsible for this difference. Thus, adaptation tools that are flexible to adjust to seasonal climate differences are needed.

Manuscript 3 showed that enhancing the cutting frequency of grassland from two to four cuts per year neither buffered, nor amplified the negative effects of increased intra-annual precipitation variability on grassland productivity. Although more frequent cutting generally increased the biomass production in the first year of the study, and led to seasonally different responses in biomass (marginally increased until July, 32% decrease until September) in the second year, no interactions between cutting frequency and precipitation variability were

found. However, the leaf N concentration of the grass species *Alopecurus pratensis* was more responsive to increased precipitation variability when cut four times a year. This effect appeared only short-term, right at the end of the drought and was not any more visible at the end of growing season. Thus, increased intra-annual precipitation variability with a longer dry period affected forage quality of grassland with higher cutting frequency more, although only short-term. Furthermore, this thesis revealed, that increasing the cutting frequency had no buffering effects on grassland productivity in the face of increased intra-annual precipitation variability.

How is it possible to improve the integration of biological data from precipitation manipulation experiments into climate change models?

During the last years, precipitation manipulation experiments became more common. They are an excellent tool to examine biological processes in the face of altered precipitation regimes due to climate change (**Manuscript 4**, De Boeck et al. 2015). However, running meta-analyses or integrating the abundance of experimentally obtained data into models proved to be difficult because of the different experimental designs and approaches with several artefacts (Beier et al. 2012 and Section 2.5). Furthermore, **Manuscript 6** highlights that often, processes commonly measured in the field, here exemplarily discussed are carbon assimilation and productivity, phenology, decomposition of soil organic matter, and plant community dynamics, are not compatible with their model analogs. This effect hinders model development and might lead to incorrect projections. **Manuscript 6** shows that the usefulness of field experiments for models can be increased if several aspects are considered: First of all, field experiments should be designed and conducted with models in mind. By increasing the discussion between the different communities and involving modelers when designing the experiment, necessary and important processes and parameters can be included from the start. Especially the application of routine measurements of basic variables e.g. soil moisture and micrometeorological data in high temporal and spatial resolution, soil water retention curves, respiration rates, plant functional types would aid in the incorporation of more sophisticated data into models. **Manuscript 6** recommends experimental designs with multiple treatment levels to cover the regression of responses across a broad range of values. Furthermore, the uncertainty of model projections with high spatial resolution should be improved by prioritizing experiments in unrepresented biomes. The modeling community can help to point out regions that show the highest uncertainty. In addition, long-term experiments (>10 years) or experiments capturing extremes are valuable for validation and improvement of temporal resolution in climate change models. **Manuscript 6** comments on modeling studies that should not be deterred from including and re-parametrizing processes evaluated in the field that lead to an initial bad model fit. It is more important to get the right causality for a given mechanism and to increase model realism. Increasing studies to improve the formulation and/or parameterization are able to reveal that the more realistic model is indeed better than a model version that omits certain mechanisms but performs better initially. In conclusion, understanding how terrestrial ecosystems will respond in future climate change, further experiments are needed which are designed by researchers of both communities heeding the recommendations above. Additionally, findings of this thesis should be considered in climate change models: contrasting plant-plant interactions between grassland species when modelling plant

community dynamics (**Manuscript 4**) and seasonality and timing of climatic factors which can lead to divergent ecological responses (**Manuscript 1**).

General conclusion

The increase of intra-annual precipitation variability is decreasing the aboveground productivity of mesic temperate grassland – particularly when it coincides with low annual precipitation amounts. Neither winter nor summer warming is amplifying or buffering the observed precipitation effects on productivity. The community composition is changing due to the altered precipitation regime favouring forbs over grasses. Complementary plant-plant interactions and dominance shifts contribute to the direction of the change. Thus, if the global climate change continues to increase intra- and interannual precipitation variability, mesic temperate grassland will likely experience large biomass losses and vegetation shifts. Adaptation strategies have yet to be found which are also flexible enough to respond to the seasonality of extreme weather events. The tested management tools of fertilisation with delayed harvest and increased of cutting frequency are not effective for buffering negative effects of increased intra-annual precipitation variability on extensively managed grassland. However, the observed alteration in community composition leads to a general increase in the forage quality. Therefore, grassland communities, which have a higher diversity in species and functional traits, seem to have the potential to partly buffer negative effects of higher precipitation variability and increasing diversity could be one adaptation tool to be studied further. This thesis shows that short-term field experiments, testing single climate factors (here: precipitation, temperature) including their variation in intensity and frequency, are useful to identify processes such as alteration in biotic interactions. The manipulation of non-uniform instead of uniform warming especially revealed a divergent response in plant performance. The combined manipulation of climate factors, as done here, shows a more realistic ecosystem response and is needed to show if climate effects on ecosystems are amplified or buffered. The co-ordinated distribution of these experiments, and the application of standardized methods and routine measurements of basic variables, can improve the incorporation of more sophisticated data into meta-analyses and climate change models. Thus, for better projections on the global consequences of climate change for ecosystems and society, more long-term, multi-factor manipulation experiments (precipitation, temperature, CO_2 enrichment), specifically designed jointly by modellers and field ecologists, are needed.

5 Emerging research challenges

This thesis could only target certain aspects of research on the effects of increased climate variability on grassland ecosystems and possible adaptation strategies. However, several important questions and further research challenges arise from the findings of this thesis. These questions are grouped into three categories: 1) vegetation shifts, 2) biotic interactions, and 3) adaptation strategies.

Does increased climatic variability cause lasting vegetation shifts?

Manuscript 1 & 2 showed that increased intra-annual precipitation variability shifted the plant community composition of temperate grassland. It is not yet clear, whether the observed species re-ordering by the altered precipitation pattern already indicated a crossing of an extreme response threshold with a significant and lasting change in the community composition (Smith 2011, Section 2.2). It could also have been a result of demographic processes to stabilize and maintain the performance (Lloret et al. 2012, Section 2.2). Long-term observation, exceeding the five years of this study, are needed to see, if natural fluctuations in species population influenced the observed pattern of the shift or if it was indeed a lasting vegetation shift. Larger experimental plots are especially needed to exclude potential species re-invasion from the matrix around the plots. This might have hindered species extinction caused by increased precipitation variability. Furthermore, this thesis showed that warmer summers coinciding with spring or summer drought likely promoted the establishment of specialists and drought tolerant species. Analyses on the species level such as an indicator species analysis should be run to verify this statement and to reveal what kind of species traits were beneficial in the face of increased precipitation variability. Therefore, root morphology and growth dynamics should especially be addressed which could be affected by the repeated soil water stress. Moreover, findings of Backhaus et al. (2014) indicate that low climate variability in the history of experimental grassland communities was of a disadvantage when facing a very severe drought. How important is the experience of climate variability for the resistance and resilience of plant species and for maintaining ecosystem functioning? How much climate variability do plant species need and what is too much? Where is the threshold between plant species adaptation to climate variability and species extinction? In this context, dynamic effects of interacting ecological and evolutionary properties and processes have to be studied, because they can lead to speciation and rapid diversification (Shefferson & Salguero-Gómez 2015). Growing evidence suggest rapid adaptive evolution in response to climate change although its consequences on demographic processes are not yet well studied (Lavergne et al. 2010; Williams et al. 2015). For grassland ecosystems, eco-evolutionary dynamics might be especially interesting, because the life cycles of grassland species are relative short (Sala et al. 1996), and rapid evolution in response to climate change may be widespread (Jump et al. 2008). Thus, rapid life history evolution should be considered in future studies on grassland ecosystem's response to increased climate variability.

How are biotic interactions accomplishing a stabilization of mesic temperate grassland productivity in the face of increased climate variability?

This thesis revealed that complementary alteration of plant-plant interactions was one underlying factor which stabilized mesic temperate grassland productivity under increased precipitation variability (**Manuscript 4 & 5**). Are there short-term adaptation responses or long-term changes in plant physiology in response to increased climate variability? Highly frequent measurements of biotic and abiotic interactions throughout the growing season are needed as there might also be alterations in interaction and feedback with nutrient resources, microclimate, (de-)synchronisation of phenology and herbivory, and plant diseases. Special focus in future research should be on the response to combined and a fast change of plant water stress due to increased variation of soil moisture. The research on plant-plant interaction of this thesis was done in experimental grassland communities with a maximum of four plant species. Further studies have to prove if the findings hold true for semi-natural and natural temperate grassland communities with higher species richness. For example, multifactor climate variability manipulation could be combined with traditional removal experiments (Symstad & Tilman 2001; Klanderud 2005) or with experiments testing the effects of introduced species (Davis & Pelsor 2001). The method to quantify competition applied in **Manuscript 4** could not distinguish between intra- and interspecific interactions. Are interspecific interactions differing in their response to increased climate variability compared to intraspecific interactions? Which kind of interaction is more important in the face of future change? Furthermore, how are biotic interactions changing across multi-tropic levels in the face of altered precipitation regimes? To which extent does the interaction of plants with microbial species (mycorrhiza, bacteria, fungal) change with combined soil water stress?

Are diverse adaptation strategies needed to maintain different grassland services or functions?

The observed changes in grassland community composition under altered precipitation regimes (**Manuscript 1 & 2**) indicate that species and functional diversity might play a key role in adapting grasslands to altered climate variability. Increasing diversity would be not an easily applicable or flexible adaptation tool to answer to seasonal changes. It could also have huge impacts on the dynamics within the grassland ecosystem. The consequences of assisted change of the community composition by increasing species and functional richness have to be assessed first. Furthermore, species or provenances, which are resilient to increased climate variability or which have beneficial traits, have to be identified and their usability for animal diet has to be tested before it could be introduced into the grassland. However, the important question which arose is what kind of ecosystem service or function should be preserved in mesic temperate grassland – biomass production, biodiversity or specific and endangered species? And how much cost and effort is allowed to maintain these aims (e.g. installation of irrigation system)? Adaptation strategies will very likely differ for these specific services or functions. The adaptation strategies probably also depend on the management intensity of the grassland system addressed (extensive vs. intensive). Interregional and international analyses have to identify the conservation aims and areas and re-evaluate the given conservation goals in respect of climate change. If maintaining grassland productivity and quality is intended, then the high productive, intensively managed

grassland systems have to be studied in more detail. Here, changing the community composition (e.g. increasing legume proportion or introducing new species) is realizable because planting of new pastures and re-seeding are common practices (Rieder 1983; Diepolder et al. 2006). Introducing the best adapted species would be easily applicable. However, simultaneously increasing diversity, especially genetic diversity, would also allow for buffering of unexpected weather events or plant diseases. When focusing on the conservation of single plant species in extensively used, mesic temperate grassland, the life-cycle, abiotic requirements, and biotic interactions of these specific species have to be studied. This geoecological view might point out ideas for adaptation strategies.

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7 Manuscripts

Manuscript 1

Importance of seasonality for the response of a mesic temperate grassland to precipitation variability and warming

Manuscript 2

Water stress due to increased intra-annual precipitation variability reduced forage yield but raised forage quality of a temperate grassland

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Increased rainfall variability reduces biomass and forage quality of temperate grassland largely independent of mowing frequency

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Extreme weather events and plant-plant interactions – Shifts between competition and facilitation among grassland species in the face of drought and heavy rainfall

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Climatic extremes lead to species-specific legume facilitation in an experimental temperate grassland

Manuscript 6

Toward a better integration of biological data from precipitation manipulation experiments into earth system models

Manuscript 1

Importance of seasonality for response of a mesic temperate grassland to precipitation variability and warming

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Importance of seasonality for the response of a mesic temperate grassland to increased precipitation variability and warming

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Running head: Importance of seasonality of climatic factors

Keywords: climate variability, seasonality, vegetation shift, EVENT II experiment, extreme weather event, precipitation regime, plant functional type, non-uniform warming, community composition, aboveground productivity

Abstract

Timing of extreme weather events within the growing season and the non-uniformity of warming might be decisive for alterations in productivity and community composition, with consequences for ecosystem functioning.

The responses of aboveground production, community composition, functional group and species evenness to altered intra-annual precipitation variability (including spring or summer drought combined with heavy rain pulses compared to regular irrigations*)* and their interactions with winter or summer warming were examined in a mesic temperate grassland.

Increased precipitation variability with spring drought resulted in a 17% reduction in ANPP, with a late drought reducing ANPP by 18% compared to regular rainfall patterns throughout the entire growing season. Winter warming increased ANPP by 12% while summer warming showed no significant effect on biomass but decreased species richness.

Both, winter warming and high precipitation variability with spring drought events, favored forbs over grasses. Less variable precipitation regimes during warmer summers favoured an even distribution of species. However, warmer summers coinciding with spring or summer drought led to reduced species evenness and likely promoted the establishment of specialists and drought tolerant species.

Seasonality of climatic factors, here early vs. late drought events in the high precipitation variability treatments, was important in driving the shifts in community composition but not for decreases in ANPP. Non-uniform warming, here winter vs. summer, affected the direction of response of both, community composition and ANPP.

The seasonality of climate change might indirectly affect ecosystem processes and species interactions and should receive more attention in climate change research.

Introduction

Increasing temperatures accompanied by more extreme precipitation regimes due to global climate change (IPCC 2014) are expected to strongly impact community composition and ecosystem functioning (Rustad et al. 2001; Knapp et al. 2008; Fay et al. 2011; Sala et al. 2015). Greater intra-annual precipitation variability can be expressed as longer dry periods

and more intense rainfall events within the growing season (Easterling et al. 2000). This change in the intra-seasonal hydroclimate will increase soil moisture variability leading to increased plant water stress and therefore to alterations in plant productivity (Fay et al. 2003, 2011; Grant et al. 2014a). Furthermore, these climatic alterations might act as a driving force in species turnover and as ecological filters in determining persistence, recruitment, and local extinction of species (Tilman & El Haddi 1992; Kammer 2002; Adler et al. 2006). Thus, increased frequency and altered timing of extreme weather events might induce shifts in community composition (Stampfli & Zeiter 2008). Besides the increase in precipitation variability, there are also variations in the rate of warming on diurnal and seasonal timescales (Xia et al. 2014). Recently, a synthesis of global air temperature data has shown non-uniform trends in the seasonal temperature change: air temperature has increased faster in winter than in summer in northern mid and high latitudes. Xia and others (2014) states that predicting the effects of non-uniform warming on ecosystems, for example on carbon cycling, is currently not possible because existing temperature experiments manipulated mostly continuous or uniform warming. However, there are indications that warming does not affect ecosystem processes equally within a growing season. Evidence suggests that ecosystem processes are stimulated by warming, particularly during cooler parts of the growing season, but not during warmer and water-limited periods (De Boeck et al. 2007; Fay et al. 2011; Hoeppner & Dukes 2012; Schuerings et al. 2013). Warmer winters with altered frost regimes can also shift plant community composition (Joseph & Henry 2008; Kreyling 2010; Kreyling et al. 2010). Potential mechanisms include altered nutrient uptake and productivity after increased freeze-thaw-cycles (Kreyling et al. 2010). Kreyling and others (2011b) have shown that short-term fluctuations in winter temperatures with increased freeze-thaw-cycles have already induced long-term shifts in species abundance distributions, with grasses benefiting the most. Findings on effects of higher temperatures in summer on community composition and functioning are controversial. When experimental warming induces moisture stress or coincides with drought, plant biomass and photosynthesis decrease (De Boeck et al. 2008; Kardol et al. 2010; Cantarel et al. 2013). Hoeppner and Dukes (2012) found that forb biomass was increased under warming with ambient precipitation conditions but decreased with a combination of warming and doubled precipitation.

Climate change experiments incorporating variability and extremes in addition to changes in mean climatic conditions, or varying the timing of climatic extremes are rare (Jentsch et al. 2007; Knapp et al. 2008; Thompson et al. 2013; Xia et al. 2014). Particularly, the interplay between factors such as warming and intra-annual precipitation variability may alter impacts on vegetation performance, and may create threshold changes in ecosystem structure (Kreyling 2010; Fay et al. 2011). The few existing multi-factor climate change experiments generally imply that combined effects are not predictable based on the response to single drivers (Shaw et al. 2002; Larsen et al. 2011; Dieleman et al. 2012). Species respond differently to changing resources, temperature, or disturbance regimes, which can lead to shifts in species dominance and composition (Sternberg et al. 1999). These changes in plant community composition and diversity, especially due to the interaction of climatic trends and extreme weather events, could buffer or alter ecosystem structure and functioning (Kardol et al. 2010). Therefore, studies examining ecosystem responses to multiple, interacting climatic drivers and to their variation in timing are needed to better understand underlying processes (Hoeppner & Dukes 2012; Wilcox et al. 2015).

Here, we experimentally study the consequences of increased precipitation variability, including extreme drought and heavy rainfall events early or late in the growing season, and non-uniform warming on productivity and composition of a semi-natural, mesic temperate

grassland. We focus on mesic temperate grassland because mesic ecosystems are expected to be particularly susceptible to more extreme precipitation regimes (Knapp et al. 2008).

Our hypotheses for semi-natural, mesic temperate grassland are:

(I) Increased intra-annual precipitation variability decreases aboveground productivity and changes the community composition of mesic temperate grassland, though this effect will differ with the timing of extreme drought periods

(II) Winter or summer warming determines changes in aboveground productivity: higher winter temperatures increase and higher summer temperatures decrease the aboveground productivity in mesic temperate grasslands

(III) Warming alters the shifts in grassland community composition and productivity in response to increased intra-annual precipitation variability

Methods

Study site

The study is part of the EVENT II experiment, where precipitation patterns and warming were experimentally modified. It was conducted in the Ecological-Botanical Garden of the University of Bayreuth, Germany (49°55'19" N, 11°34'55" E, 365 m a.s.l.). The regional climate is characterized as temperate and moderately continental with a mean annual air temperature of 8.2 °C and 724 mm mean annual precipitation (1971-2000, data from German Weather Service). The soil of the site is a Gleysol (Glaser and others, 2013). The homogeneous, loamy Ap horizon (42% sand, 43% silt, 15% clay) has a depth of 0.3 m followed by a clayey Bg horizon. The groundwater table drops to between -1.5 and -2.0 m during summer and can reach up to -0.3 m in winter and after longer rainfall periods. The main rooting zone is within the upper 0.15 m and hardly any roots penetrate the Bg horizon. The mean pH of the topsoil is 4.1 (1 M KCl). Permanent wilting point is around 15 vol% soil moisture content. The experimental site is a semi-natural grassland which has not been ploughed for at least 20 years and not fertilized for more than 20 years prior to the installation of the experiment in 2008. Prior to the start of the EVENT II experiment, the meadow was mown twice a year for hay production. The grassland community is dominated by tall grasses such as *Alopecurus pratensis* L. (meadow foxtail) and *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl (tall oat-grass). Most common herb species are *Cerastium holosteoides* Fr. (mouse ear chickweed) and *Plantago lanceolata* L. (ribwort plantain) and the most abundant legume is *Trifolium pratense* L. (red clover). The meadow harbors on average 14 species m^{-2}. All species are C3 species.

Experimental design

The field experiment was carried out in a two-factorial design manipulating (1) intra-annual precipitation variability (low, medium, high – with two variants of high which included drought events combined with heavy rain spells either early or late in the growing season) and (2) warming (ambient, winter warming, summer warming). The design consisted of 60 plots, each 1.5 m x 1.5 m in size, with every factorial combination repeated five times. Within each precipitation variability manipulation, warmed and not warmed plots were blocked and randomly assigned.

Precipitation variability

For the manipulation of the intra-annual precipitation variability, the annual amount of precipitation was kept constant since 2009, while the precipitation pattern in time was altered during the growing season (April – September). Thus, the following treatments were realized:
In the low precipitation variability treatment (lowVar), the plots received at least the long-term (1971-2000) precipitation sum per week. The plots were exposed to ambient rainfall. If ambient rainfall was less than the long-term average sum of the same week, the missing amount of rainfall was added manually. If weekly rainfall exceeded the long-term sum, it was not subtracted from the next irrigation. The precipitation amount of the low precipitation variability treatment served as reference amount for all other treatments.
Plots of the medium precipitation variability (medVar) remained under ambient precipitation conditions except for additional irrigations at four times (before and after spring drought, after summer drought, and in late September close to the end of the growing season) in order to compensate differences with lowVar precipitation amounts at those times. These rainfall additions were also made for the two high variability treatments, resulting in the same annual amount of precipitation for all treatments.
High precipitation variability was simulated by an extreme drought event early ($highVar_{early}$) or late ($highVar_{late}$) in the growing season. The drought event was always followed by a heavy rainfall event. The duration of the drought event was set to a 1000 year recurrence event calculated by Gumbel statistics based on the 1961-2000 time series of a local weather station (No. 04070). Drought was defined as the number of consecutive days with <1 mm daily precipitation. Accordingly, natural rainfall was excluded for 42 days using rain-out shelters. The rain-out shelters were constructed with steel frames (Hochtunnel, E & R Stolte GmbH, Germany) and covered with transparent plastic sheets (material: 0.2 mm polyethylene, SPR 5, Hermann Meyer KG, Germany) during the drought period that permitted nearly 90% penetration of photosynthetically active radiation according to tests prior to set-up. The plastic sheets started from a height of 80 cm above the ground to allow near-surface air exchange, which reduced microclimatic artefacts, such as increased temperatures or reduced wind speed. The excluded amount of rainfall was applied together with the adjustment to the reference amount at the end of the artificial drought period as one heavy rain event within two or three days.
We calculated the coefficient of variation CV (= standard deviation/daily mean*100) for precipitation and soil moisture to test variability strength of the precipitation treatments (Table 1). For all years the intra-annual variability of precipitation was altered, resulting in lowest variability in lowVar, intermediate variability in medVar, and high variability in treatments which included a spring drought ($highVar_{early}$) and summer drought ($highVar_{late.}$). The change of precipitation variability resulted in consistently altered soil moisture variability except in years 2010 and 2011. In 2010, CV of soil moisture in $highVar_{early}$ was lower than in medVar. In 2011, soil moisture variability of medVar was the same as in $highVar_{late}$.

Table 1 Coefficient of variation (CV) of daily precipitation amounts and soil moisture

		Precipitation variability			
	Year	Low	Medium	$High_{early}$	$High_{late}$
CV precipitation	2008	177	188	197	199
	2009	201	243	277	299
	2010	231	269	306	295
	2011	219	251	353	401
	2012	192	234	334	285
	all	207	244	308	318
CV soil moisture	2008	20	29	37	42
	2009	24	26	30	29
	2010	21	31	26	32
	2011	28	32	40	32
	2012	37	45	48	53
	all	30	37	40	40

Warming manipulation

According to differing seasonal temperature change observations and projections (IPCC 2014; Xia et al. 2014), warming manipulations were performed either during the winter (October – March) or during summer (April – September) starting in October 2009. Temperatures were increased using overhead infra-red heating lamps equipped with reflector domes (IOT/90 250W Elstein, Northeim, Germany) at a height of 0.8 m theoretically resulting in 60 W $plot^{-1}$ (Table 2). Lamps were raised to 1 m when tall grasses reached 80 cm. Plots not warmed were equipped with dummy heaters. Air temperature at 5 cm above ground was raised on average by 0.9 °C in winter and by 1.3 °C in summer (Table 2). Soil temperature at -2 cm was raised by 1.5 °C in winter and by 0.6 °C in summer, respectively. To avoid possible edge effects created by temperature gradients with distance from the lamp, all data collection took place in the center of each plot directly below the lamp.

Data collection

Soil moisture, soil temperature and air temperature

Soil moisture was logged every hour using frequency domain (FD)-sensors (ECH_2O, Decagon devices, Pullman, USA). The loggers were installed in undisturbed soil in the main rooting zone (-2 to -7 cm) in all plots. The soil moisture data was calculated from the average of all five replicates for each treatment except when missing data occurred due to sensor or logger errors (Fig. 1). Soil temperature (-2 cm) and air temperature (+5 cm) was measured hourly in one warmed and one not warmed plot per precipitation variability treatment by thermistors (B57863-106 S302-F40, EPCOS AG, München, Germany).

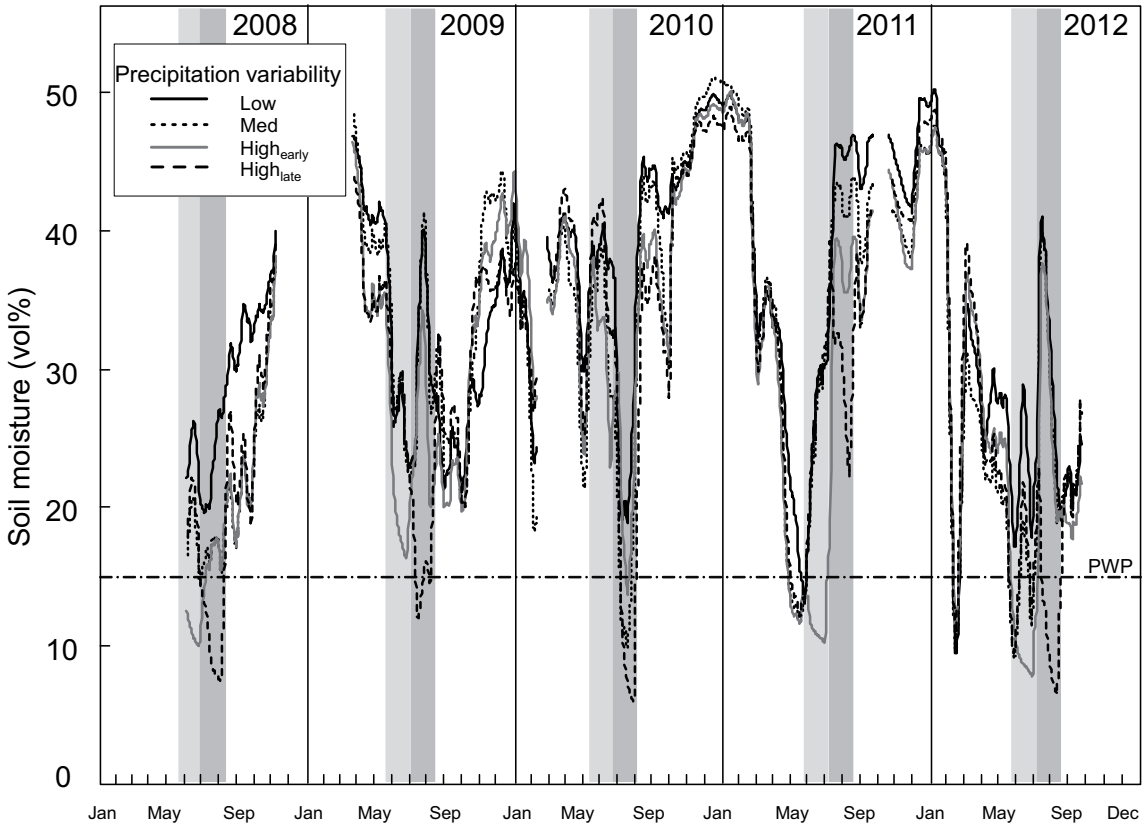

Figure 1 Soil moisture dynamics for the precipitation variability treatments low, medium, early and late high for the years 2008-2012; Given are two-week running means of soil moisture; Grey shaded areas (light grey: spring drought, dark grey: summer drought) mark periods of rainfall exclusion by means of rainout shelters; Dotted horizontal line indicates permanent wilting point (PWP).

Aboveground biomass

For aboveground biomass, harvests of the grassland took place twice every year (at the end of the early drought treatment in June and at the end of the growing season in September), resembling local agricultural routines for extensively used grassland. For every harvest, a steel frame (0.1 m²) was randomly placed twice in the central part of each plot, so that two samples of plant material were taken per plot. All aboveground standing plant material was cut 3 cm above soil surface within the steel frame. One sample of plant material was sorted to functional groups – grasses, forbs, and legumes – and the other was sorted to species. All plant material was dried to a constant weight at 60 °C and then weighed (Ohaus NavigatorTM, Ohaus Corporation, Parsippany, USA; accuracy ± 0.01 g). For aboveground net primary productivity of species ($ANPP_{Spec}$) the species biomass of both harvests within every year was summed per species and plot. For aboveground net primary productivity of functional groups ($ANPP_{FG}$), biomass of the functional group samples of every plot and of both harvests within a year were added to the biomass of species belonging to this functional group. Total aboveground net primary productivity (ANPP) is the sum of biomass for all plant samples within one plot for each year based on sampling 0.2 m².

Table 2 Mean air (+5 cm) and soil (-2 cm) temperatures, and coefficient of variation of temperatures (CV) in warmed and not warmed (ambient) grassland plots for summers and winters (2010-2012) and the respective temperature change due to warming. Given are mean seasonal temperature values and standard errors

	Season	Year	Ambient mean temperature (°C)	Warming mean temperature (°C)	Temperature change (°C)	CV ambient	CV warming	Dates
Air temperature	Summer	2010	14.5 ± 0.5	15.4 ± 0.4	0.8	29	27	09-Apr-2010 – 04-Oct-2010
	Summer	2011	16.0 ± 0.3	17.5 ± 0.3	1.5	22	20	09-Apr-2011 – 11-Oct-2011
	Summer	2012	16.4 ± 0.4	18.0 ± 0.4	1.6	28	26	06-Apr-2012 – 11-Oct-2012
	Winter	2009/2010	1.7 ± 0.4	2.3 ± 0.4	0.6	216	273	16-Oct-2009 – 08-Apr-2010
	Winter	2010/2011	3.0 ± 0.3	4.0 ± 0.3	1.0	111	134	10-Oct-2010 – 08-Apr-2011
	Winter	2011/2012	2.5 ± 0.3	3.8 ± 0.3	1.3	107	135	12-Oct-2011 – 05-Apr-2012
Soil temperature	Summer	2010	14.3 ± 0.4	15.0 ± 0.4	0.7	27	25	09-Apr-2010 – 04-Oct-2010
	Summer	2011	16.0 ± 0.3	16.7 ± 0.2	0.7	21	19	09-Apr-2011 – 11-Oct-2011
	Summer	2012	16.3 ± 0.3	16.9 ± 0.3	0.6	26	25	06-Apr-2012 – 11-Oct-2012
	Winter	2009/2010	2.8 ± 0.3	3.9 ± 0.3	1.1	101	125	16-Oct-2009 – 08-Apr-2010
	Winter	2010/2011	3.0 ± 0.3	4.5 ± 0.3	1.5	90	117	10-Oct-2010 – 08-Apr-2011
	Winter	2011/2012	2.2 ± 0.2	4.3 ± 0.3	2.1	79	130	12-Oct-2011 – 05-Apr-2012

Evenness & richness

The evenness of plant species biomass was calculated using the Pielou's evenness index (J) for each plot and year: J= H/ ln(S) where S is the species richness (number of species in the community) and H is the Shannon diversity ($H=-\sum p_i * \ln(p_i)$ where p_i is the fractional biomass of each species). J is constrained between 0 and 1 and it decreases with increasing variation between species fractional biomass in the community. Additionally, we calculated the Pielou's evenness to determine functional group evenness per plot using $ANPP_{FG}$ instead of $ANPP_{Spec}$.

Statistical analyses

We performed linear mixed effect models in combination with analyses of variance (ANOVA) to test for effects of altered precipitation variability and warming manipulation and their respective interaction on the response variables. The model was simplified by using precipitation variability and warming manipulation as fixed factors, if no significant interaction was found. The split-plot design was taken into account by adding repetition (which accounts for blocking the warming treatments within the rainfall variability treatments) as random factor in the model (Faraway 2006). Pre-analyses with year as fixed factor showed no significant interacting effects of precipitation variability and warming on all response parameter. Therefore, year was added to the model as random factor to take repeated measures into account. Residual versus fitted plots and plots showing sample quantiles versus theoretical quantiles based on the model were checked for homogenous variance and normal distribution of residuals to validate the linear mixed effect models (Faraway 2006). If conditions of normality were not met or if data required an improved homogeneity of variance, data were transformed using log or exponentiation by five. In all tests, the level of significance was set to $p = 0.05$. All statistical analyses were performed using the statistical software R 2.4.1 (R Development Core Team 2006). For linear mixed effect models and multiple post-hoc comparisons the software package "lme4" version 0.9975-13 and "multcomp" version 0.992-1 were used respectively.

Results

Effects of increased rainfall variability and warming on aboveground net primary productivity

Alteration of intra-annual precipitation variability led to significant changes in the aboveground net primary productivity (ANPP) of grassland communities ($F = 9.9$, $p < 0.001$, Fig. 2a). Over the five-year study period, ANPP in the low precipitation variability treatment (lowVar) was higher than ANPP in all other, more variable, precipitation patterns ($F = 14.5$, $p < 0.001$).

The warming treatment significantly altered the aboveground net primary productivity of grassland communities ($F = 6.2$, $p = 0.014$): Higher temperatures in winter led to higher biomass production by about 12% ($p < 0.001$, Fig. 2b), whereas summer warming did not significantly increase biomass ($p = 0.237$) compared to ambient conditions.

The effects of altered precipitation variability and warming on ANPP were independent from each other ($F = 2.0$, $p = 0.065$).

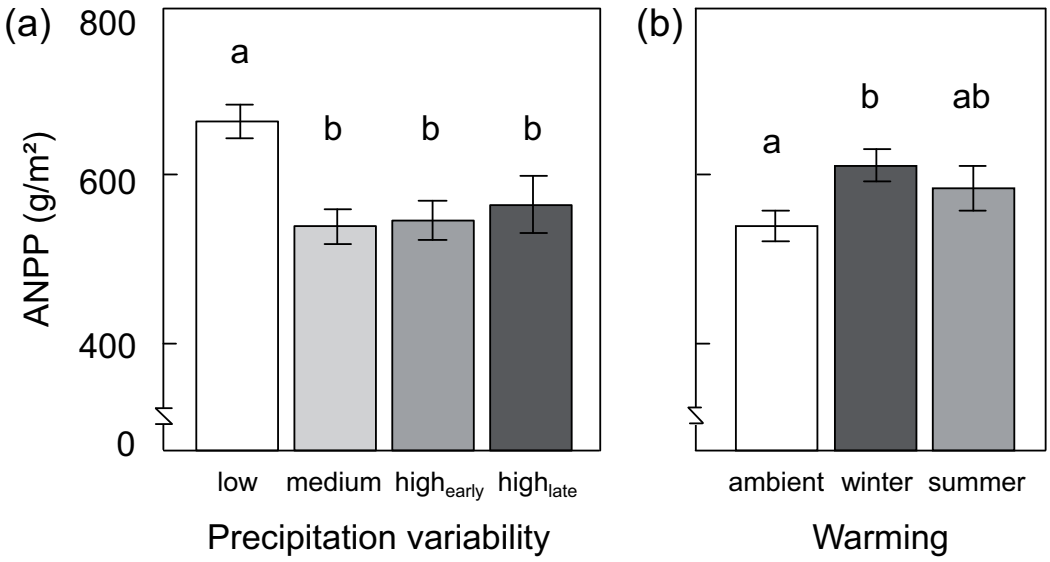

Figure 2 Aboveground net primary productivity (ANPP) for (a) altered intra-annual precipitation variability (low, medium, high including early drought & heavy rainfall events, and high including late drought & rainfall events) and (b) warming treatment (ambient, winter, summer): Given are mean values of the years 2010-2012 and standard error; Lower case letters mark homogeneous groups according to post-Hoc tests; No significant interaction between the precipitation variability and warming was found.

Effects of altered precipitation variability and warming on the performance of grasses, forbs and legumes

We found changes in the ANPP of all functional groups – grasses, forbs and legumes – due to altered precipitation variability (Fig. 3a): ANPP of grasses was decreased both by highVar$_{early}$ (-35%, $p < 0.001$) and highVar$_{late}$ (-32%, $p < 0.001$) compared to lowVar. ANPP of forbs was increased by 55% ($p = 0.038$) compared to lowVar. Additionally, ANPP of legumes was reduced by both, highVar$_{early}$ and highVar$_{late}$, compared to medVar ($p = 0.039$ and $p = 0.026$) but not compared to lowVar.

Warming effects on the aboveground net primary productivity of functional groups differed between the seasons of warming (Fig. 3b). Forb biomass was in average 18% higher in winter-warmed grassland compared to summer-warmed grassland ($p = 0.015$). Grasses and legumes showed no significant response to the warming treatments (grasses: $F = 0.8$, $p = 0.400$, legumes: $F = 2.2$, $p = 0.114$). There was no significant interaction between altered rainfall pattern and warming on ANPP of the three functional groups (grasses: $F = 1.8$ $p = 0.100$, forbs: $F = 1.6$, $p = 0.152$, legumes: $F = 2.0$, $p = 0.071$).

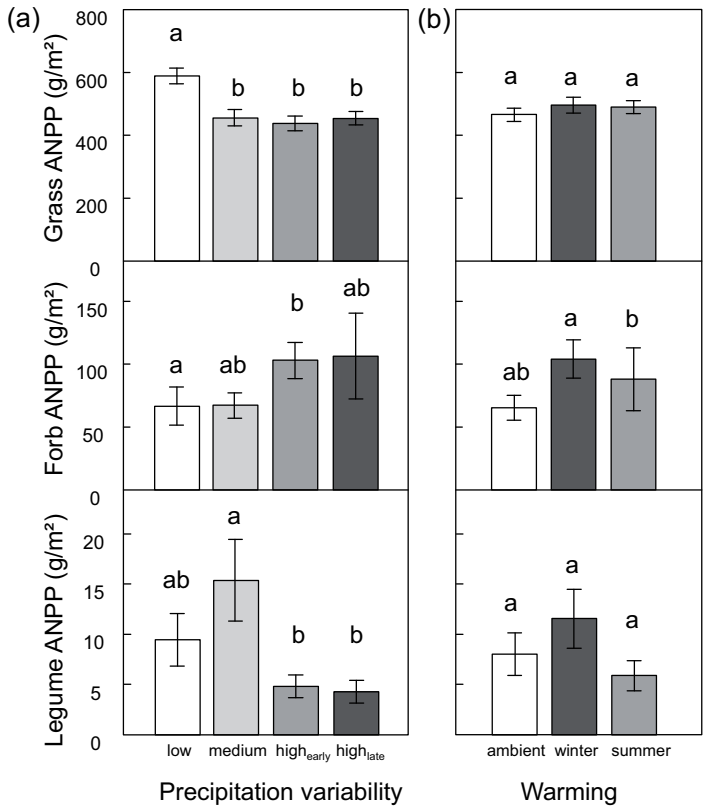

Figure 3 Aboveground net primary productivity (ANPP) of the functional groups grasses, forbs and legumes for (a) the intra-annual precipitation variability treatments (low, medium, high including early drought & heavy rain events, and high including late drought & heavy rain events) and (b) the warming treatment (ambient, winter, summer); Given are mean values of the years 2010-2012 and standard errors; Lower case letters mark homogenous groups according to post-Hoc tests. No significant interaction between the precipitation variability and warming treatments was found.

Effects of altered precipitation variability and warming on species richness, functional group evenness and species evenness

Species richness was not altered by changing intra-annual precipitation variability ($F = 1.8$, $p = 0.142$, Fig. 4a). However, altered precipitation variability affected functional group evenness ($F = 4.1$, $p = 0.008$, Fig. 4c). Functional groups were less variable when the grassland was exposed to $highVar_{early}$ compared to lowVar ($p = 0.028$). Species evenness responded differently to altered precipitation variabilty compared to functional group evenness ($F = 6.0$ $p = 0.001$, Fig. 4e). Species evenness in medVar and $highVar_{early}$ precipitation variability treatment was not different from lowVar. Though, species evenness was increased by $highVar_{late}$ ($p < 0.001$).

Warming led to differences in species richness ($F = 13.9$, $p < 0.001$, Fig. 4b). Summer-warmed grassland had two species less compared to ambient or winter-warmed grassland (both $p < 0.001$). No differences in species richness were found in the two years before the warming treatment started. Furthermore, warming affected the functional group eveness ($F = 4.0$, $p = 0.021$, Fig. 4d) and species evenness ($F = 6.5$ $p = 0.002$, Fig. 4f). For both functional groups and species, evenness was increased by winter warming compared to summer warming (Fig. 4 d, f).

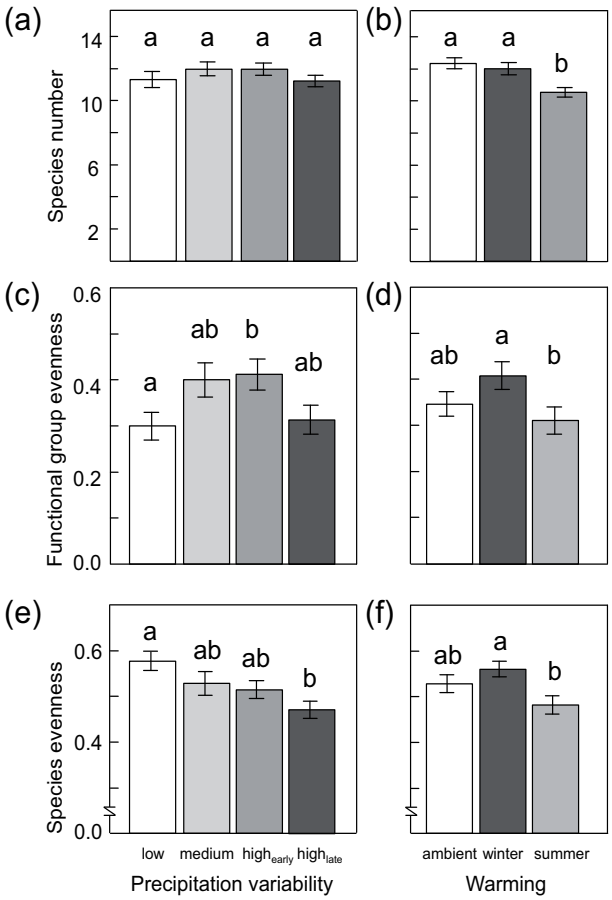

Figure 4 Species richness (a, b), functional group (c, d) and species (e, f) evenness in the manipulated grassland for the intra-annual precipitation variability treatments (low, medium, high including early drought & heavy rain events, and high including late drought & heavy rain events) and the warming treatment (ambient, winter, summer); Given are mean values of the years 2010-2012 and standard error; Lower case letters mark homogenous groups according to post-Hoc tests; No significant interaction between the precipitation variability and warming was found for species richness and functional group evenness; For interactive effects of precipitation variability and warming treatment on species evenness see Figure 5.

There was no interaction between precipitation variability and warming on species richness ($F = 1.2$, $p = 0.285$). An interaction was found for functional group evenness ($F = 2.2$, $p = 0.049$): functional group variability was lower in winter-warmed grassland under medium precipitation variability compared to lowVar ($p < 0.010$). Precipitation variability and warming had also interactive effects on species evenness ($F = 4.8$, $p < 0.001$, Fig. 5): in summer-warmed grassland, species evenness was highest under low precipitation variability.

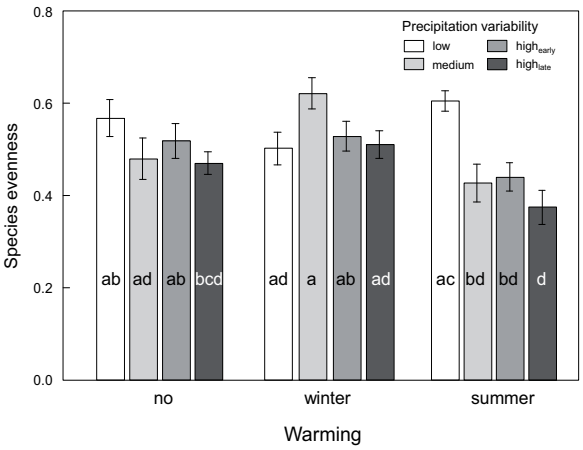

Figure 5 Species evenness in the manipulated grassland for the intra-annual precipitation variability treatments (low, medium, early high and late high) within the three warming treatments (ambient, winter, summer); Given are mean values of the years 2010-2012 and standard error; Lower case letters mark homogenous groups according to post-Hoc tests.

Discussion

Effects of altered intra-annual precipitation variability on aboveground net primary productivity

We found that increased intra-annual precipitation variability decreased aboveground productivity in this mesic temperate grassland. The main reason for the decrease in ANPP seems to be the amplified fluctuation in plant water availability in the high precipitation variability treatments. This effect was verified by the CV of soil moisture content. The length and occurrence of plant water stress was enhanced due to the larger intervals between the rainfall events in the high variability treatments which included a spring drought ($highVar_{early}$) or a summer drought ($highVar_{late.}$). Comparably, the continuous water supply in the lowVar treatment reduced the soil moisture variability. The observed soil moisture change also confirmed the proposition by Knapp and others (2008), that the usually moist soils of mesic ecosystems will experience greater drying by the extreme changes in precipitation regime. In consequence, plants of these mesic systems, which are more or less adapted to sufficient rainfall throughout the year, and to infrequent drought stress, will be increasingly stressed. A reduction of aboveground productivity, as observed here, in combination with stomatal regulations, are possible mechanisms to save water under drought stress (De Boeck et al. 2006). Furthermore, Fay and others (2011) suggested that their observed reduction of ANPP might be an indicator for lower ecosystem rainfall use efficiency due to the increased intra-annual soil moisture variability. Our finding of a decrease in aboveground net primary productivity due to increased intra-annual rainfall variability is comparable to other studies: Knapp and others (2002) and Fay and others (2003, 2011) found reductions in ANPP of a temperate grassland ecosystem, when the intervals between natural rain events were extended by 50% and the collected and stored rain falling during these intervals was reapplied as single large events.

Effects of altered intra-annual precipitation variability on grassland composition

Forbs benefited from high intra-annual precipitation variability characterized by a spring drought event ($highVar_{early}$) whereas grass biomass decreased. Likely reasons for this varying behaviour of plant functional types to altered precipitation patterns are different plant adaptation strategies and growth forms, such as rhizomatous structure, leaf structure, and bud position, but also a different timing of phenological stages (Sternberg et al. 1999; Kammer 2002). Here, soil moisture variability was increased. Therefore, grasses with shallow and fibrous roots, which are usually concentrated in the upper part of soil profiles are more vulnerable to drought related soil moisture variability when compared to deep rooted plants e.g. tap-rooted forbs (Fay et al. 2003; Morecroft et al. 2004). The deeper root distribution of forbs is beneficial to access deeper, less temporally variable soil water supplies and thus may explain the increased forb biomass in this study (compare Fay and others (2003)). Thus, root structures adapted to effectively exploit water under changing environmental conditions exhibited by forb species are useful when drought or enhanced rainfalls occur.

Another factor favouring forb production over grasses under increased precipitation variability might have been its different germination strategy and therefore recruitment. Germination was shown to be affected by precipitation variability (Robinson & Gross 2010). According to Stampfli and Zeiter (2004) grasses are less successful in re-colonizing after drought because of fewer and short-lived seeds in seed banks compared to forbs. We compared the seed

bank types according to Thompson and others (1997) of our grass and forb species and could confirm this assumption: Seeds of our grass species persist on average less than one year whereas seeds of our forb species persist between one and five years. Drought might also enable seedlings of different species to establish in a dense grass sward where usually the establishment of new seedlings is virtually non-existent (Grime et al. 1994; Sternberg et al. 1999).
Furthermore, the observed reduction of the dominant grasses was in accordance with dominance shifts in other studies where dominant species were less drought tolerant than subdominant species (Hillebrand et al. 2008; Stampfli & Zeiter 2008; Kardol et al. 2010). The shifts in the community composition visible in the alteration of grass and forb biomass were supported by the alteration of functional group evenness due to altered precipitation variability. With the increase of forbs and a decrease of grasses the functional groups became more evenly distributed within the community. Kardol and others (2010) found higher evenness in their dry relative to their wet treatment after changes in the dominance structure of the community. High evenness including high trait variance causes better adaptive capacity and is ecologically important in order to sustain long-term productivity in changing environments (Norberg et al. 2001; Hillebrand et al. 2008). Consistent with this general assumption, the $highVar_{late}$ treatment in our study showed reduced functional evenness and decreased productivity under increased precipitation variability. A trend of similar direction for $highVar_{early}$ however was not significant. Hillebrand and others (2008) state that a reduction of evenness might cause problems as synergistic plant-plant interactions collapse when the community pattern shifts towards the dominance of one species. Hence, the increase in evenness under early drought events might be beneficial to adapt to further drought events. Moreover, the increased functional group evenness but unchanged species richness at $highVar_{early}$ indicates that a former subdominant forb species likely increased their biomass in the same amount as the formerly dominant grass species lost their biomass.

Importance of seasonality of extreme events for productivity and composition of grassland communities

Seasonality of the extreme events, here spring vs. summer drought, in the high precipitation variability treatments, was not important for decreases in total ANPP. In both treatments, total ANPP was equally reduced. This effect is connected with the response of the dominant functional group: ANPP of grasses was reduced by both, high precipitation variability with spring and summer drought event. The higher soil moisture variability with increased precipitation variability was probably the main driver for the grass species response, though not for the other functional groups as forbs and legumes showed no reductions in productivity in the face of high precipitation variability. However, the increase of forb productivity only in $highVar_{early}$ indicates that other factors were likely generating this different response besides higher soil moisture variability. Reasons for this benefit of forbs seems to be the reduced competitive pressure by decreasing, water stressed grasses (Grant et al. 2014b). This shift in plant-plant interaction might facilitate the expression of different traits such as varying germination phenology, seedling emergences, reproduction strategies and success, timing of resource uptake, and drought tolerances (Kammer 2002; Fay et al. 2003; Stampfli & Zeiter 2008; Craine et al. 2010).
Furthermore, only the treatment with the late summer drought event increased the variability of species in combination with higher temperatures. Higher temperatures coinciding with

reduced rainfall and increased transpirational demand from the high canopy can cause a gap between soil moisture supply and evaporation demand resulting in performance losses (Knapp et al. 2002). Besides, this response to late drought events might indicate the facilitation of, or competition on, single species though not on certain functional groups. Reduced species evenness is seen to be responsible for a decrease of the temporal stability of communities (Hillebrand et al. 2008; Isbell et al. 2009), and could therefore indicate higher risks under late drought events. Additionally, Orwin and others (2014) showed that species evenness was important for multiple ecosystem functions (e.g. plant biomass production, ecosystem gas exchange, water retention, leaching of DOC and N). Thus, the reduced species evenness due to high precipitation variability with late summer drought events ($highVar_{late}$) might indicate that grassland functions beyond productivity were affected.

Effects of winter and summer warming on ANPP

The separation of winter and summer warming revealed that the non-uniform warming is decisive for changes in aboveground productivity. Total ANPP increased only due to higher winter temperatures. The increased winter temperatures have likely caused an extension of the growing season by advancing canopy green-up in spring, changing plant phenology (earlier timing of bud-break, flowering and later leaf senescence) and stimulating productivity at the same time (Rustad et al. 2001; Fay et al. 2011). The increase in ANPP due to winter warming in our study is comparable to findings of Hutchison and Henry (2010) and Schuerings and others (2013). They showed that a warmer winter initiated an earlier start to the growing season which was primarily responsible for the positive overall effect of warming on plant productivity. Temperature variability increased with winter warming (not with summer warming, see Table 2). This is because winter warming reduced the insulating snow cover, leading to increased temperature variability (Kreyling 2010). In our case, this increased temperature variability did not reduce plant growth due to frost damage, an effect reported for colder climates (Bokhorst et al. 2009).
We hypothesized a decrease in ANPP by summer warming as several studies found decreased plant productivity due to warming which coincided with lower soil water contents (De Boeck et al. 2007; Hoeppner & Dukes 2012). The realized temperature increases (air: 1.3 K, soil: 0.6 K) were likely not severe enough to cause severe soil water stress. Thus, the grassland ANPP was resistant towards the manipulated summer warming.

Effects of winter and summer warming on grassland community composition

Here, non-uniform warming led to opposite effects of winter versus summer warming on species and functional group evenness. Higher temperature in winter increased forb biomass compared to summer warming, and contributed to the higher total ANPP in the winter warming treatment. Unusual warm temperatures in spring can affect the growth and biomass of subdominant forb species in temperate grassland, likely due to a changed competitive pressure by the dominant species (Kammer 2002). This is in accordance with Dostálek and Frantík (2011) and Sternberg and others (1999) who found that grass cover decreases if higher temperatures during winter cause early spring drought, thereby enabling the colonisation and establishment of other species in the newly formed gaps in the sward. However, we did not observe short-term drought events caused by the winter warming and grass biomass was also not altered by winter warming. Therefore, the advantage of forbs was likely caused by other, not biomass-density related factors. Here, higher winter

temperatures reduced snow cover and increased temperature variability. Short-term fluctuations in winter temperature, which also caused shifts in community composition in a study by Kreyling and others (2011b), could be responsible for the increase of forb productivity. The reduced insulation by snow cover might also have led to species-specific frost damages. Winter-hardiness of herbaceous plants is generally determined by vegetative rather than reproductive structures (Šimkūnas et al. 2013). Differences in vegetative anatomy might therefore have resulted in varying frost damage on grasses and forbs. Similar to the response observed to the soil moisture variability, the root morphology and root exposure to soil temperature variability in the upper soil layer, could be decisive for the advantage of forbs under winter warming.
Furthermore, species richness was reduced by summer warming indicating that some species were not able to cope with the higher temperatures. The lack of ANPP response in all functional groups to summer warming together with a slight decrease of evenness suggested that some subdominant species must have been lost.

Interactive effects of altered intra-annual precipitation variability and summer warming on grassland composition

In this study precipitation variability and warming effects were additive. This is contrary to findings by Hoeppner and Dukes (2012) who showed that ANPP of forbs was increased due to warming under ambient weather conditions though decreased in combination with wet conditions. However, we found that species evenness was decreased when summer warming coincided with increased precipitation variability. Thus, whereas warmer and more humid, low variability weather conditions favoured an even distribution of species, the higher variance in species under summer warming and extreme precipitation variability probably promoted the establishment of specialized plant species which tolerate extreme events and quickly adapt to variable precipitation patterns. Given the call for more complex scenarios including interactions between different climatic parameters (Kreyling & Beier 2013), and the non-additive results obtained in the few multi-factor climate change experiments (Shaw et al. 2002; Larsen et al. 2011; Hoeppner & Dukes 2012; Dieleman et al. 2012), our results for largely additive effects of precipitation variability and non-uniform warming are quite remarkable.

Conclusion

Timing of climatic events, here winter vs. summer warming and early vs. late drought events in the high precipitation variability treatments, was decisive for productivity and community composition of a mesic, temperate grassland. Both high precipitation variability treatments decreased total ANPP compared to low precipitation variability, but only one ($highVar_{early}$) changed the functional composition of the grassland. Furthermore, the opposite shifts in grassland functional composition to summer and winter warming emphasize the ecological importance of the non-uniformity of climate warming. Here, winter warming and high precipitation variability with a drought event early in the growing season favored the forb species, and these effects were additive. The observed shift in species composition can have indirect consequences for other ecosystem processes across multiple trophic levels. Beside altered biotic interactions due to dominance shifts, changes in community composition are able to cause alteration in e.g. the forage value (Grant et al. 2014a), and consequently

nutrient cycling, of these managed grasslands. Therefore, climate change experiments should recognize the seasonality and timing of climatic factors depending on the projections of their study region because their ecological effects might be divergent. Furthermore, neglecting the timing of climatic factors might hide underlying processes which are important to reveal for understanding and mitigating climate change.

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Manuscript 2

Water stress due to increased intra-annual precipitation variability reduced forage yield but raised forage quality of a temperate grassland

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Water stress due to increased intra-annual precipitation variability reduced forage yield but raised forage quality of a temperate grassland

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Abstract

Due to climate change an increase in the intra-annual precipitation variability including extreme drought and heavy rainfall events is predicted to impact major ecosystem processes. Evidence suggests that crop and forage production will be affected by altered climate variability. Due to the growing human population and rising demand for high quality animal feed it is necessary to determine the consequence of increased precipitation variability on forage yield and quality in order to adapt or implement compensation strategies against possible negative effects.

Here, we present data from a field experiment in which a temperate European grassland was subjected to altered intra-annual precipitation variability (low, medium, high) in interaction with management strategies namely fertilization and alteration of harvest date (delay by 10 days). We measured forage yield and root length, quantified parameters of forage quality (crude protein, crude fiber, crude ash, crude fat, sugar, neutral detergent fiber (NDF), acid detergent fiber (ADF), in vitro gas production) and estimated Relative Feed Value, net energy for lactation and metabolizable energy. Additionally, we tested the influence of seasonality of extreme weather events on the responsiveness of forage yield and quality to management strategies.

Increased intra-annual precipitation variability decreased forage yield of the grassland. Furthermore, the proportion of functional groups was altered towards less grass and more forb biomass with amplified precipitation variability. Increased crude protein content and reduced fiber content (crude fiber, NDF, ADF) with increasing precipitation variability improved the Relative Feed Values. Crude protein content was enhanced by fertilization during drought but reduced by delayed harvest after the drought period. Fertilization reduced losses in grassland annual yield caused by extreme precipitation. Management strategies proved less effective if precipitation variability occurred later in the season than earlier in the season.

A nitrogen dilution effect (decreased plant nitrogen concentration with increasing shoot biomass) likely influenced the grassland crude protein contents under altered precipitation regimes and might have masked possible effects of precipitation variability on plant nitrogen and therefore on quality of grassland species. Nevertheless, alterations in the plant community composition and plant senescence seem to be the main drivers of forage quality change. Fertilization during drought periods and harvest delay after drought periods were only partially successful as management strategies to sustain forage production in more extreme precipitation regimes of the future. Further strategies need to be developed that

acknowledge the shift in plant species compositions as the main driver of changes in forage quality in the face of changing precipitation patterns.

1. Introduction

Intra-annual precipitation variability is predicted to increase due to global warming, leading to longer dry periods and more intense rainfall events with strong impacts on agriculture and food security (Jentsch & Beierkuhnlein 2008; Fay et al. 2011; IPCC 2012). Greater precipitation variability increases soil moisture variability, which leads to increased plant water stress and therefore alters grassland productivity (Nippert et al. 2006; Heisler-White et al. 2008; Fay 2009). Forage and crop production will be altered directly through climatic changes and indirectly through changes in nutrient availability, resulting in higher yield variability and altered forage quality (Buxton 1996; Olesen et al. 2011). Livestock production, which depends on grazing or the use of fresh forage, will in turn also be affected by alterations of climate variability (Olesen et al. 2011). With steadily rising demand for food and high quality animal feed it is important to determine the consequences of increased precipitation variability on forage production so that animal requirements are met and the vulnerability of markets to price swings can be reduced (Buxton 1996; Bruinenberg et al. 2002; Huyghe et al. 2008; Battisti & Naylor 2009).

In the absence of weather extremes the most important factor influencing the forage quality of a given species is the plant maturity stage, i.e. its phenology (Buxton 1996). With advancing maturity and increasing age within a given growing season, forage quality declines (Ball et al. 2001; Bruinenberg et al. 2002). This is reflected by a decrease in digestibility of plant components and declining nitrogen content, due to altered leaf/stem ratio and increasing fiber content (Collins & Casler 1990; Bruinenberg et al. 2002; Hopkins & Wilkins 2006). Furthermore, forage of different plant functional groups differ in their phenological development of feeding value and digestibility (Duru et al. 2008). Legumes are of higher forage quality and their digestibility decreases over time at a slower rate than the digestibility of grasses (Buxton 1996; Ball et al. 2001). Plant development and therefore forage quality depends on abiotic factors such as temperature, water availability, solar radiation, and soil nutrient status (Buxton 1996; Andueza et al. 2010). Rising temperature leads to increased rates of plant development, alterations of plant chemical composition, and to reductions of the leaf/stem ratio and digestibility (Buxton 1996; Ansquer et al. 2009). Rising spring temperatures in particular strongly interact with advancing plant maturity and lead to higher variation and faster decline in nutritive value than high temperatures later in the summer (Buxton 1996; Cop et al., 2009a).

Moderate water deficit slows plant maturation, and if it does not cause severe leaf loss, forage quality and digestibility can be maintained or even slightly improved (Buxton 1996; Reddy et al. 2003). However, long and extreme drought events inhibit tillering and branching, accelerate the death of tillers and senescence of leaves, and relocate protein, nitrogen, and soluble carbohydrates from leaves to roots, reducing the nutritive value of the plant (Buxton 1996; Durand et al. 2010). Drought also affects the nitrogen nutrition of aboveground plant parts due to reduced uptake and use of soil mineral nitrogen (Durand et al. 2010). Nonetheless, protein content was found to increase under drought in plants in symbiosis with arbuscular mycorrhizal fungi (Subramanian & Charest 1995). In some species, sugar and proline are accumulated with water stress, the latter improving the recovery of plants from drought (Saglam et al. 2008).

With global climate change, forage quality of grasslands will not only be altered directly via changes in abiotic factors governing plant growth and development, but also via alterations in the community composition (Stampfli & Zeiter 2004; Kreyling et al. 2011a). The nutritive value of grassland is strongly influenced by community composition mainly due to strong variation in species identities, chemical composition, phenological stages, functional groups, and photosynthetical pathways (Huyghe et al. 2008; Cop et al. 2009a; Andueza et al. 2010). Although increased species richness can ensure the stability of biomass yield, differences in nutritive value are more related to species composition and functional group proportions than to species number (Baumont et al. 2008; Sanderson 2010). For instance, crude protein content of mixed-species grasslands is controlled by the legume component due to its ability to fix atmospheric nitrogen, and the fiber content by the grass proportion (Sanderson 2010).
In the light of potential direct and indirect effects of climate change on forage production there is an urgent need to develop adaptation or compensation strategies to ensure high forage yield and quality under increasing precipitation variability. Generally, strategies to cope with increasing variability will differ from strategies to adapt to trends of mean climatic conditions (Battisti & Naylor 2009; Olesen et al. 2011). Since variability and mean climatic conditions will likely change together these strategies must be comprehensive. Possible management strategies include specific species mixtures, schemes of fertilizer application, irrigation techniques, and cutting regime. It might be helpful to identify or breed key species varieties with improved drought resistance (Beierkuhnlein et al. 2011) or that maintain forage quality at advanced stages of maturity (Buxton 1996).
Fertilizer, especially nitrogen, is known to affect yield, functional community composition and forage quality (Cop et al., 2009b). In addition, fertilization can change the proportion of leaves (Duru et al. 2008). Besides raising crude protein content, decreasing fiber content and improving digestibility, the timing of N fertilization and the amount of fertilization could be used to improve drought resistance. N uptake is reduced during drought (Durand et al. 2010), though the uptake rates of plant nutrients such as ammonium and nitrate can rise rapidly within a few days after N starvation (Lee & Rudge 1986). Thus, higher nutrient availability due to fertilization may ensure an even quicker recovery of plant tissue, and thereby forage quality after the drought period. In the absence of drought, a 1-week delay in harvesting decreases digestibility and crude protein content and increases fiber concentration of forage (Buxton 1996; Bruinenberg et al. 2002). A delay of harvest after a rewetting period following drought might therefore provide enough time to improve the nutrient availability for plants. Furthermore, harvest delay, especially in combination with fertilization during drought may allow plants to recover tissue and forage quality by promoting new leaf development and relocating nutrients from roots to leaves.
Here, we experimentally studied the consequences of increased precipitation variability on the forage yield and quality of a temperate grassland in Central Europe. We further tested two management strategies, namely fertilization during drought periods and delayed harvest after the drought periods. Together, these strategies aim to recover forage quality and yield after drought periods.

Thus, our hypotheses are as follows

(I) Increased intra-annual precipitation variability decreases the yield and quality of forage in temperate, semi-natural grasslands.
(II) A 10-day delay of harvest after drought periods increases forage yield and quality, in particular if accompanied by fertilization during the drought period, compared to a grassland which is harvested immediately after drought periods.

2. Methods

2.1. Study site

The study is part of the EVENT II experiment which tests the effects of altered precipitation regimes in interaction with land use methods on the ecosystem functions of semi-natural grassland. It is located in the Ecological-Botanical Garden of the University of Bayreuth, Germany (49°55'19'' N, 11°34'55'' E, 365 m asl). The regional climate is characterized as temperate and moderately continental with a mean annual air temperature of 8.2 °C and 724 mm of mean annual precipitation (1971-2000, data from German Weather Service). The soil of the experiment is classified as Gleysol (Glaser et al., 2013) with a homogeneous, loamy Ap horizon of 30 cm depth (42% sand, 43% silt, 15% clay) and a clayey Bg horizon. The groundwater table drops to -1.5 to -2 m during summer and can reach up to -30 cm in winter and after long rain periods. Roots grow primarily within the upper 15 cm, with hardly any roots penetrating the B horizon. The mean pH of the topsoil is 4.1 (1 M KCl). Permanent wilting point is around 15 vol.% soil moisture content and field capacity is around 40 vol.%. The experimental site is a semi-natural meadow which has not been ploughed for at least 25 years and not fertilized for more than 20 years prior to the installation of the experiment in 2008. Prior to the start of the EVENT II experiment, the meadow was mown twice a year for hay production. The semi-natural grassland community is dominated by tall grasses such as *Alopecurus pratensis* L. (meadow foxtail) and *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl (tall oat-grass). Grasses form 75 - 85% of the total biomass, whereas the percentage of forb species varies between 15 and 23%. There are legume species within this grassland though their contribution to the biomass yield is below 2%. All species are C3 species concerning their photosynthetic pathway.

Table 1 Timing and amounts of compensation irrigations (mm) on the plots of the medium (medVar), early ($highVar_{early}$) and late high ($highVar_{late}$) precipitation variability treatments given to apply the same overall rainfall amount as the reference plots (low precipitation variability treatment, lowVar, in mm), and ambient rainfall amounts (mm) in the corresponding manipulation periods for the years 2010 and 2011

Year	Manipulation period	Reference precipitation amount (lowVar)	Ambient precipitation	Irrigation date	Irrigation amount		
					medVar	$highVar_{early}$	$highVar_{late}$
2010	01/04-10/05	70.5	42.8	May 10th	27.7	27.7	27.7
	11/05-23/06	157.0	138.8	June 23rd	18.2	138#	18.2
	24/06-03/08	156.1	94.6	August 3rd	61.5	61.5	151.7#
	04/08-27/09	219.1	201.6	September 27th	17.5	17.5	17.5
2011	01/04-23/05	89.8	36.9	May 23rd	52.9	52.9	52.9
	24/05-04/07	191.5	165.2	July 4th	26.3	191.4°	26.3
	05/07-15/08	229.9	196.0	August 15th	33.9	33.9	229.9°
	16/08-03/10	130.3	99.0	October 3rd	31.3	31.3	31.3

#applied on three consecutive days °applied on two consecutive days

2.2. Experimental design

The field experiment was carried out in a three-factorial design manipulating (1) intra-annual precipitation variability (low, medium, early high, late high, roof artifact control), (2) fertilization (fertilizer addition, control), and (3) timing of harvest (directly after drought period, 10-day delay after drought period). The design consisted of 100 plots, each 75 x 75 cm in size, separated by lateral barriers of stainless steel down to -25 cm, with every factorial combination repeated five times. Within each precipitation variability manipulation, application of fertilizer and delay of harvest were blocked and randomly assigned.

2.2.1. Precipitation variability

For the manipulation of the intra-annual precipitation variability, the annual amount of precipitation was kept constant, while the precipitation pattern was altered during the growing season (April – September). Thus, the following treatments were realized:

In the low precipitation variability treatment (lowVar), the plots received at least the long-term (1971-2000) precipitation sum per week. If natural rainfall was less than the long-term average sum for the same week, the missing amount was added using tap water and portable irrigation systems (Kreyling et al. 2008). If weekly rainfall exceeded the long-term sum, it was not subtracted for the next irrigation. The precipitation amount of the low precipitation variability treatment served as a reference amount for all other treatments.

The medium precipitation variability (medVar) plots received ambient precipitation, but were irrigated additionally four times (before and after spring drought, after summer drought, and in late September, Table 1) in order to adjust total precipitation amount to the reference amount (lowVar) at those times. These additions were also made for the two high variability treatments, resulting in the same annual amount of precipitation for all treatments.

Both extreme precipitation variability treatments, early high precipitation variability ($highVar_{early}$) and late high precipitation variability ($highVar_{late}$), were exposed to a 1000-year drought event (in late spring and summer, respectively). This was calculated by Gumbel statistics and based on the 1961-2000 year time series of a local weather station. The manipulation was done by excluding natural rainfall for 42 days using rain-out shelters as described in Walter et al. (2012). Rain-out shelters covered grassland in $highVar_{early}$ from 13/05 to 22/06/2010 and $highVar_{late}$ from 22/06 to 02/08/2010 (24/05 – 04/07/2011 and 05/07 – 15/08/2011, respectively). The excluded amount of rainfall was applied together with the adjustment to the reference amount at the end of the artificial drought period as one heavy rainfall event within two or three days.

Additionally, we ran a rain-out shelter artifact control (artCon). These plots were covered by the same rain-out shelters as used for both high variability treatments during the spring drought of the $highVar_{early}$ treatment, but they were irrigated below the shelters with the same precipitation amounts as the medium variability treatment after every rainfall.

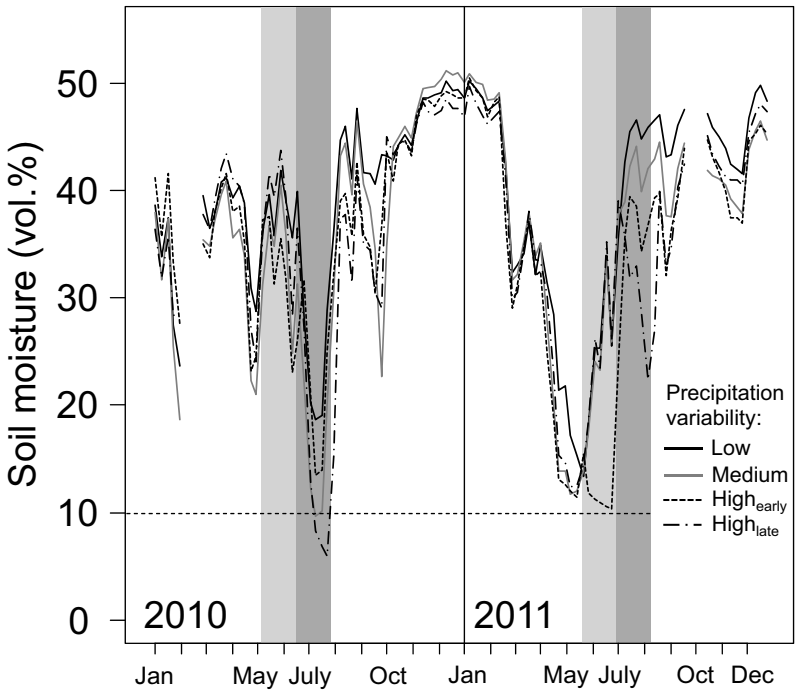

Figure 1 Soil moisture dynamics for the precipitation variability treatments low, medium, early and late high for the years 2010 and 2011. Given are weekly running means of soil moisture. Grey shaded areas (light grey: late spring drought, dark grey: summer drought) mark periods of rainfall exclusion by means of rainout shelters. Dotted horizontal lines show permanent wilting point (PWP) and field capacity (FC) of the soil in the experiment

2.2.2. Effectiveness of the precipitation variability treatments: Precipitation and soil moisture

To test the strength of variability of the precipitation treatment, we calculated the coefficient of variation CV (= standard deviation*mean^{-1}*100) of precipitation and soil moisture.
The intra-annual variability of precipitation was altered resulting in lowest variability in lowVar, intermediate variability in medVar and highest variability in highVar$_{early}$ and highVar$_{late}$ (see Table 2). The degree of variability of the early and late extreme precipitation variability treatments differed within the two years of study. In 2010, highVar$_{early}$ had the most variable intra-annual precipitation. In 2011, highVar$_{late}$ was most variable and nearly twice as variable as lowVar. Figure 1 shows the soil water dynamics within the two year study period for the different precipitation variability treatments. For the majority of the growing season (April – September) the low precipitation variability treatment had the highest soil moisture. Furthermore, lowVar had less days below the permanent wilting point and shorter duration of plant water stress than the other precipitation variability treatments in both years (Table 3). Outside of the growing season, soil moisture of the different precipitation variability treatments showed only small differences. The coefficients of variation for soil moisture show that soil moisture was also the least variable in the lowVar treatment (Table 2). However, in 2010 the medVar treatment was more variable than the highVar$_{early}$ treatment and in both years as variable as the highVar$_{late}$ treatment. Additionally, medVar had more days below permanent wilting point and longer plant water stress period than highVar$_{early}$ in 2010 (Table 3). The field experimental site exhibits a clay soil that is influenced by ground- and stagnant water. In late spring 2010, high ambient rainfall amounts during the manipulation of drought (highVar$_{early}$) led to higher ground water table. The high ground water table in combination with higher irrigation amount in highVar$_{early}$ at the end of the drought caused that medVar had lower soil moisture in late summer compared to highVar$_{early}$. Thus, there is a higher

coefficient of variation value for medVar than for highVar$_{early}$. A drainage system to avoid such conditions could not be installed without disturbing or destroying the long-term established semi-natural grassland. However, the differences in variability between the low precipitation variability treatment and both extreme precipitation variability treatments are well expressed in the CV of precipitation and soil moisture. Thus, differences in response parameters between these treatments can be related to plant stress due to soil moisture variability.

Table 2 Coefficient of variation (CV) of daily precipitation amounts and soil moisture for the precipitation variability treatments low, medium, early high (high$_{early}$) and late high (high$_{late}$) for each year of the study

		Precipitation variability			
	Year	Low	Medium	High$_{early}$	High$_{late}$
CV Precipitation	2010	231	266	302	291
	2011	217	251	353	401
	mean	224	259	328	346
CV Soil moisture	2010	21	32	26	32
	2011	28	31	40	32
	mean	25	32	33	32

Table 3 Characterization of plant water stress for the precipitation variability treatments low, medium, early high (high$_{early}$) and late high (high$_{late}$) for each year of the study in terms of number of days below or equal permanent wilting point (PWP=15 vol.%), number of days below or equal 50% of plant available water, and longest period of plant water stress (= consecutive days below or equal PWP)

Plant water stress	**Year**	**Precipitation variability**			
		Low	Medium	High$_{early}$	High$_{late}$
Number of days ≤ PWP (≤15.0 vol.%)	2010	1	23	11	31
	2011	15	30	70	30
Number of days ≤ 50% plant available water (≤ 27.5 vol.%)	2010	29	56	58	49
	2011	57	69	92	79
Duration of longest water stress period (consecutive days ≤ 15 vol.%)	2010	1	18	6	31
	2011	7	9	40	9

2.2.3. Fertilization

Half of the plots were fertilized once every year on the 30th day of spring drought in all precipitation variability treatments (except in the plots of the late extreme variability (highVar$_{late}$) which were fertilized later) using a common, water soluble, mineral NPK fertilizer "Linzer Top S/Cl" (12/12/17 +2 MgO + 5 S with boron and zinc) (Linzer Agro Trade GmbH, Linz, Austria). Nitrogen content was 4.9% nitrate and 7.1% ammonium, phosphorus content was 9.6% P_2O_5 and neutral-ammoncitrate, water soluble phosphate. Potassium was water soluble K_2O. Further, the percentage of boron was 0.05% and 0.015% for zinc. We

homogenously applied 14 g of the granulate fertilizer on the plots which equals an amount of 249 kg ha^{-1} a^{-1} fertilizer in total, including 30 kg ha^{-1} a^{-1} N, 30 kg ha^{-1} a^{-1} P_2O_5 and 42 kg ha^{-1} a^{-1} K_2O. Half of the plots of the late extreme variability treatment were fertilized on the 30th day of the summer drought.

2.2.4. Delay of harvest

One fertilized and one unfertilized plot of each precipitation variability treatment (except the late extreme variability treatment) were harvested at the end of the early drought in July and the other two plots, one fertilized and one not fertilized, were mowed ten days later. The plots of the late extreme variability treatment ($highVar_{late}$) were cut at the end of the summer drought mid of August and 10 days later, respectively. All plots were harvested a second time without delay at the end of the growing season in September.

2.3. Data collection

2.3.1. Soil moisture

Soil moisture was logged every hour using frequency domain (FD)-sensors (ECH_2O, Decagon devices, Pullman, USA). The loggers were installed in undisturbed soil in the main rooting zone (-2 to -7 cm) in unfertilized plots without delayed harvest of every precipitation variability treatment in five repetitions. The soil moisture data was calculated from the average of all five replicates for each treatment except when missing data occurred due to sensor or logger errors.

2.3.2. Forage yield

For forage yield data, harvests of the grassland took place twice a year (at the end of the drought and at the end of the growing season in September). For every harvest, a steel frame (0.1 m²) was randomly placed twice in the center of each plot. All aboveground standing plant material was cut 3 cm above soil surface within the steel frame. The plant material was sorted to functional groups – grasses, forbs, and legumes – and dried to a constant weight at 60 °C and then weighed (Ohaus NavigatorTM, Ohaus Corporation, Parsippany, USA; accuracy ± 0.01 g). For forage yield, the biomass of the first harvest within each of the two years (2010 & 2011) of this study was summed for each functional group and for the total plot, respectively. For total year yield, total biomass of both harvests within each year was summed.

2.3.3. Root length

Root length as a proxy for below-ground biomass production was acquired using the minirhizotron-technique. Transparent plastic tubes (5 cm diameter) were installed in each plot to a depth of 45 cm at a 45-degree angle one year before the start of this study. The aboveground portion of the tube was covered with opaque silver foil. In the first year, images of 3.8 cm² were taken at 5 cm and 15 cm depth by a digital camera mounted on an endoscope. In the second year, a modified desktop scanner was used to obtain images of the roots in the depth of 0 to 20 cm. Sampling dates in both years were once at the end of the spring drought and once at the end of September. The images were analyzed for root length using the line intersect method (Tennant 1975) with a systematic grid (for details see Kreyling et al. (2008)). The same grid was used for the scans and placed at the position of 5

and 15 cm soil depth on each scan. The root lengths of both depths were summed for each date.

2.3.4. Nutritive values

The dried plant material of all functional groups from the first harvest (end of drought) was re-mixed for each plot after weighing (see 2.3.2). These samples of each plot and each year (2010 and 2011) were analyzed for nutritive values (LfL, Zentrallabor Grub, Germany). Before analyses, the samples were ground to pass through a sieve of 1 mm pore size. All analyses of crude nutrients (protein, ash, fiber, sugar, fat), neutral detergent fiber (NDF), and acid detergent fiber (ADF) followed standard procedures and calibration curves given by the VDLUFA (association of German agricultural research institutes) (Naumann & Bassler 2007). For all analyses (except crude protein) near infrared reflectance spectrometry (NIRS) method was used and validated by wet chemical tests. Crude protein was determined by the Dumas combustion method. The determination of in vitro gas production, a measure for forage digestibility and energy content, was done according the Hohenheim gas test. The gas production is a value for the cumulative gasses (carbon dioxide and methane) produced in vitro with rumen liquor. Metabolizable energy (ME) for pig and cattle as well as net energy lactation (NEL) were estimated using standard equations (GfE 2008, 2009):

To compare the quality between the different precipitation treatments and between other studies, the Relative Feed Value (RFV) was calculated as follows (Collins & Fritz 2003)

$$RFV = (DDM * DMI) / 1.29 \quad \text{eqn (1)}$$

where DDM = dry matter digestibility (%) and DMI = voluntary dry matter intake (% of body weight). Dry matter digestibility and voluntary dry matter intake can be estimated with

$$DDM = 88.9 - (0.779 * ADF) \quad \text{eqn (2)}$$

$$DMI = 120 / NDF \quad \text{eqn (3)}$$

where ADF and NDF are expressed as percentage of dry matter (DM).

2.3.5. Soil mineral analysis

In the second year of this study (2011), mixed soil samples of the upper layer (0-10 cm) were taken from every plot at the end of the spring drought and analyzed for plant available nitrogen (ammonium, nitrate), potassium, phosphorus, and total carbon and nitrogen content. The soil samples were air dried and sieved (< 2 mm). For ammonium and nitrate analyses, a part of every soil sample was extracted with a 1 M KCl solution and then filtered (< 2-3 µm, Blauband 15A, AP57.1, Roth, Karlsruhe). Quantification was done by flow injection analysis (measurements conducted at BayCEER Analytical Chemistry, Bayreuth, device: FIA-LAB, MLE GmbH, Dresden, Germany). For potassium and phosphorus analyses, soil samples were extracted using diluted (1:10) solution made of 14.7 g $CaCl_2$ and 7.88 g DPTA (diethylentriaminepentaacetic acid, Merck KGaA, Darmstadt) and filtered as above. Quantification was done by flow injection analysis (measurements conducted at BayCEER Analytical Chemistry, Bayreuth, device ICP-OES VistaPRO, Varian Inc., Palo Alto, USA). For determination of total carbon and nitrogen contents, parts of all soil samples were ball-milled after sieving and measured using an element analyzer (measurements conducted at BayCEER Analytical Chemistry, Bayreuth, device: Flash EA1112, ThermoQuest, Egelsbach, Germany).

Table 4 ANOVA results of the applied linear mixed effect models carried out to test alterations by precipitation variability (PrecVar), application of fertilizer, a 10-day delay of harvests, and their interactions on yield and quality of grassland. Given are F and p-values for yield of first harvests in total and for the functional groups grasses, forbs and legumes, for total year yield, for root length, contents of crude protein fiber, ash, fat, sugar, net energy lactation, metabolizable energy pig, metabolizable energy cattle, in vitro gas production, neutral detergent fiber (NDF), acid detergent fiber (ADF) and Relative Feed Value. Significant ($p<0.05$) effects are highlighted with bold numbers

		Precipitation variability		**Fertilizer**		**Delay of harvest**		**PrecVar X Fertilizer**		**PrecVar X Delay**		**PrecVar X Fertilizer X Delay**	
		F	p	F	p	F	p	F	p	F	p	F	p
Yield	Total	15.71	**<0.0001**	5.39	**0.0223**$^{+}$	6.54	**0.0121**$^{+}$	0.84	0.4368	1.49	0.2305	0.87	0.354
	Grasses	31.57	**<0.0001**	3.25	0.0745	4.71	**0.0324**$^{+}$	0.26	0.7733	1.98	0.1429	1.81	0.1814
	Forbs	10.27	**0.0001**	0.40	0.5287	0.24	0.6265	0.55	0.5811	0.08	0.9201	0.25	0.6176
	Legumes	8.56	**0.0004**	0.00	0.9996	0.04	0.8361	0.10	0.9038	0.38	0.6880	0.18	0.6735
	Year total	8.72	**0.0003**	22.66	**<0.0001**$^{+}$	2.22	0.1394	1.26	0.2871	0.65	0.5228	0.16	0.8558
Root length		0.10	0.9019	0.64	0.4250	0.04	0.8512	1.28	0.2839	2.40	0.0956	1.35	0.2475
Crude protein		9.68	**0.0001**	107.84	**<0.0001**$^{+}$	17.49	**0.0001°**	0.39	0.6806	1.28	0.2827	0.94	0.3931
Crude fibre		33.84	**<0.0001**	0.28	0.5962	1.37	0.2450	0.10	0.9021	0.88	0.4190	0.26	0.7717
Net energy lactation		12.64	**<0.0001**	0.13	0.7167	4.99	**0.0278**$^{+}$	0.06	0.9403	1.79	0.1717	0.23	0.7916
Crude ash		5.26	**0.0068**	19.02	**<0.0001**$^{+}$	10.82	**0.0014°**	0.30	0.7401	0.17	0.8423	0.13	0.8805
Sugar		2.75	0.0688	34.44	**<0.0001°**	0.02	0.8833	0.03	0.9749	0.97	0.3839	0.00	0.9959
Crude fat		26.36	**<0.0001**	5.62	**0.0197**$^{+}$	2.21	0.1404	0.66	0.5167	1.48	0.2331	0.41	0.6670
Metabolizable energy cattle		8.24	**0.0005**	0.36	0.5504	1.06	0.3059	0.23	0.7948	1.42	0.2467	0.23	0.7950
Metabolizable energy pig		6.95	**0.0015**	5.93	**0.0167°**	3.14	0.0797	0.22	0.8047	0.57	0.5681	0.31	0.7369
Gasbildung		2.30	0.1052	1.61	0.2072	0.82	0.3682	0.08	0.9271	1.89	0.1563	0.54	0.5826
NDForg		39.21	**<0.0001**	0.58	0.4472	0.20	0.6529	0.16	0.8525	0.97	0.3819	0.57	0.5646
ADForg		16.35	**<0.0001**	0.00	0.9485	2.42	0.1232	0.17	0.8398	1.01	0.3672	0.24	0.7835
Relative Feed Value		27.72	**<0.0001**	0.23	0.6293	0.38	0.5385	0.02	0.9767	0.88	0.4199	0.61	0.5463

$^{+}$increased. °decreased by management strategy

2.4. Statistical analyses

We performed linear mixed effect models and analyses of variances (ANOVA) in order to test for significant effects of precipitation variability, fertilization, and delay of harvest on the response variables. The split plot design was taken into account by adding repetition as random factor to the model. For analyzing repeated measures, we added sampling date or year as further random factor. To validate the linear mixed effects models, residual versus fitted plots and plots showing sample quantiles versus theoretical quantiles based on the model were looked at for homogenous variance and normal distribution of residuals prior to analyses (Faraway 2006). If the assumptions of normality were not met or for improving homogeneity of variance, data was transformed using log(y+1) (legume yield) and log(y) (crude protein, ammonium). In case of significant interactions between the fixed effects (precipitation variability, fertilization, delay of harvest), Tukey's 'Honest Significant Difference' tests were run for post-hoc comparison. The level of significance was set to p=0.05 for all tests. All statistical analyses were performed using the computer program R 2.13.2 (R Developement Core Team 2011) with the additional software package "nlme" (Pinheiro et al. 2011). Statistical analyses of all response parameters did not show significant differences between the artifact control and the medium precipitation variability in combination with differences between medium and early extreme variability. Thus, we excluded artifacts of the rain-out shelters on the response parameters and consequently, removed the artifact control data from the data sets. All analyses on precipitation variability effects were run without including the late extreme treatment ($highVar_{late}$) because of different sampling dates in comparison to all other treatments. However, we run additional analyses to test the interaction of fertilizer and delay of harvest for both extreme precipitation variability treatments. For these, only both high precipitation variability treatment data remained in the data set. Here, we focused only on significant interactions of precipitation variability with fertilizer or delay of harvests and not on effects of precipitation variability itself.

3. Results

3.1. Effects of altered precipitation variability on forage yield and root length of grassland

Medium and high intra-annual precipitation variability decreased forage yield compared with low intra-annual variability but they did not differ from each other (Fig. 2a, Table 4). Responses to altered intra-annual precipitation variability differed among the functional groups. Grass yield decreased with higher precipitation variability (Fig. 2b). On the other hand, forbs produced significantly more biomass under high precipitation variability ($highVar_{early}$) compared to the low and medium precipitation variability treatment (lowVar, medVar) (Fig. 2c, Table 4). Legumes showed highest yield under medium precipitation variability (medVar) but produced little yield under low and high precipitation variability (Fig. 2d, Table 4). The root length in the upper 15 cm of the soil was not affected by altered intra-annual precipitation variability in summer (Fig. 2e, Table 4). Altered precipitation variability did not affect forage yield of second harvest at the end of growing season ($F = 0.102$, $p = 0.902$). However, the grassland could not compensate the precipitation variability effects during the remaining growing season, thus total year yields showed the same responses to altered precipitation variability as yields of summer harvest (Table 4, total year functional group yields not shown).

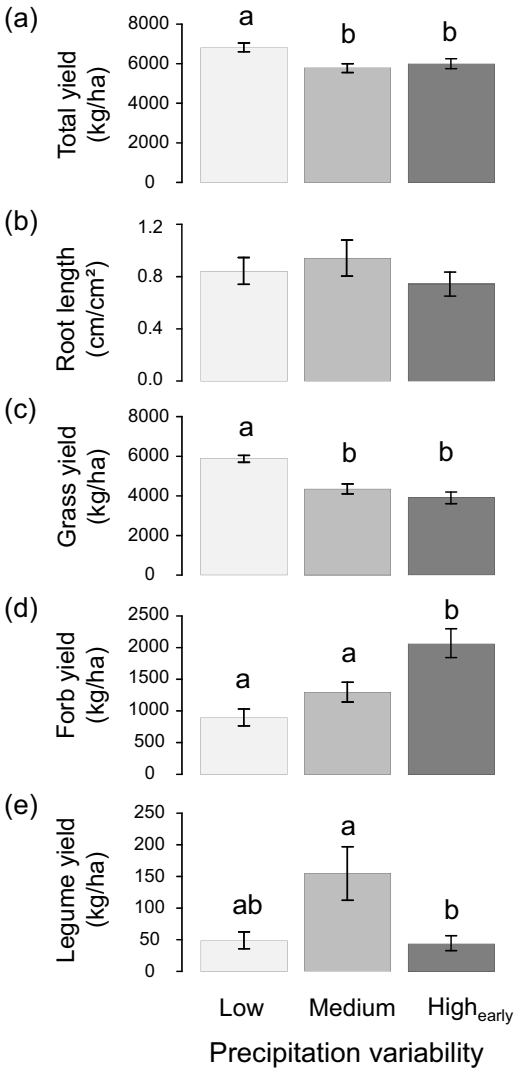

Figure 2 Effects of increasing precipitation variability (low, medium and high$_{early}$) on the forage yield and root length of grassland over two years of study. Given are mean values and standard errors of yields of first harvests (a) in total and of the functional groups (b) grasses, (c) forbs, and (d) legumes as well as (e) root length sum in the upper 15 cm at first harvest. Small letters mark significant differences ($p<0.05$) by precipitation variability resulting from linear mixed effect models

3.2. Effects of altered precipitation variability on forage quality of grassland

Over the two years of study, crude protein and crude ash content were lowest under low precipitation variability conditions and increased under medium precipitation variability (Figs 3a & 3c, Table 4). High precipitation variability did not alter crude protein and crude ash in comparison to lowVar or medVar. Crude fat, metabolizable energy for cattle and pigs, and Relative Feed Value had nearly the same mean values in medVar and highVar$_{early}$ but decreased under low precipitation variability (Figs 3e, g, h, l, Table 4). All nutritive values of fiber content of the tested grassland – crude fiber, neutral detergent fiber (NDF) and acid detergent fiber (ADF) – decreased with increasing precipitation variability from lowVar to medVar (Figs 3b, j, k, Table 4). Sugar content, net energy for lactation, and in vitro gas production were not altered by variable intra-annual precipitation variability (Figs 3d, f, i, Table 4).

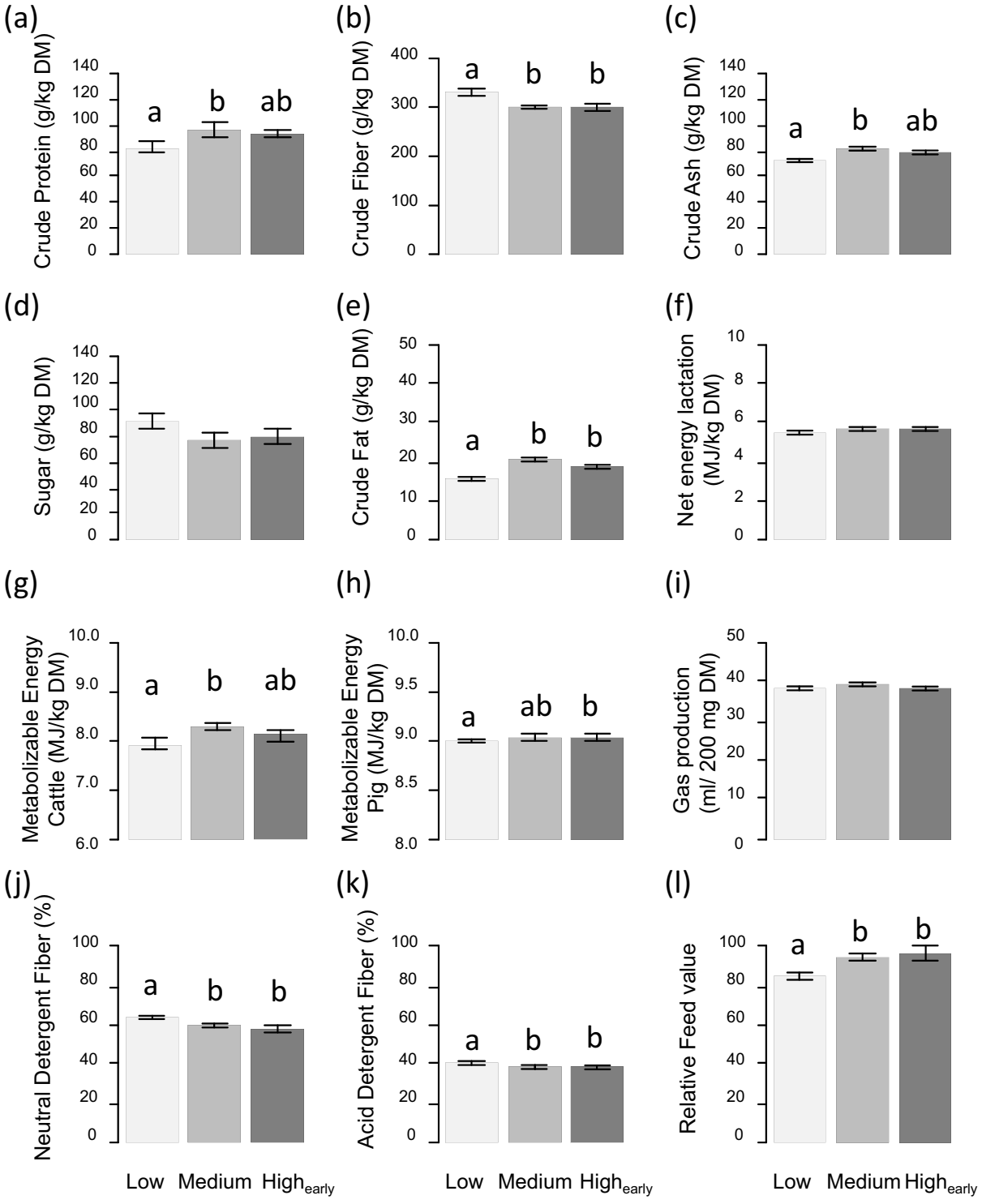

Figure 3 Effects of increasing precipitation variability (low, medium, $high_{early}$) on nutritive values of grassland over two years of study, given are mean values and standard errors of (a) crude protein, (b) crude fiber, (c) crude ash, (d) sugar, (e) crude fat, (f) net energy for lactation, (g) metabolizable energy cattle, (h) metabolizable energy pig, (i) in vitro gas production, (j) neutral detergent fiber, (k) acid detergent fiber, and (l) Relative Feed value. Small letters mark significant effects of altered precipitation variability ($p<0.05$) on the nutritive values resulting from linear mixed effect models; DM = dry matter

3.3. Effects of altered precipitation variability and fertilization on soil nutrients status

Higher precipitation variability led to a decrease of plant available nitrogen in the form of ammonium and nitrate within the soil in comparison to the lowVar treatment (Table 5). Potassium and phosphorus contents of the soil were increased by higher precipitation variability. Fertilizer raised the soil phosphorus content (Table 5). Total carbon and nitrogen content were not altered by the applied manipulation regimes.

3.4. Effects of fertilization on forage yield, quality, and Relative Feed Value of grassland

The application of fertilizer on the 30th day of the spring drought increased total forage yield (Table 4). This increase was still visible at second harvest at the end of growing season ($F = 39.21$, $p < 0.001$). Unfertilized grassland produced 6209±287 kg ha^{-1} of forage in lowVar, 5140±194 kg ha^{-1} in medVar and 5725±296 kg ha^{-1} in highVar$_{early}$ within a year. Fertilization raised year forage yield of lowVar to 7460±211 kg ha^{-1}, yield of medVar to 6437±352 kg ha^{-1}, and yield of highVar$_{early}$ to 6270±378 kg ha^{-1}, which equaled the yield values of the unfertilized grassland under low precipitation variability. Furthermore, fertilization increased the content of crude protein by 19.4 g kg^{-1} DM, crude ash by 8.3 g kg^{-1} DM and crude fat by 1 g kg^{-1} DM within the grassland. However, the content of sugar and the metabolizable energy for pigs was decreased by the application of fertilizer. Unfertilized grassland had on average 21.3 g kg^{-1} DM more sugar than fertilized grassland. The other tested nutritive values and the Relative Feed Value were not altered by additional fertilization. (Table 4)

3.5. Effects of delayed harvest on forage yield, quality, and Relative Feed Value of grassland

A 10-day delay of harvest after the spring drought and the following heavy rainfall event (re-irrigation) decreased crude protein and crude ash content in grassland by 8.1 g kg^{-1} DM and 6.2 g kg^{-1} DM, respectively, compared to immediate harvest after drought. Total forage yield and grass yields were also increased within these 10 additional days. Relative Feed Value was not altered by the delayed harvest. However, grassland that was harvested with a delay had higher net energy for lactation compared to the grassland, which was harvested right at the end of the late spring drought and heavy rainfall events. (Table 4)

3.6. Interaction of altered precipitation variability with application of fertilizer and delayed harvests

The effects of altered precipitation variability on nutritive values were not buffered or amplified by the application of fertilizer during the drought or by a 10-day delay of the harvest after the extreme drought event in late spring (Table 4). Although the response of forage yield to the interaction of fertilizer and precipitation variability was statistically not significant ($F=1.26$, $p=0.2871$), average yield of fertilized grassland in highVar$_{early}$ was on the same level as the yield of unfertilized grassland of the low precipitation variability treatment.

Table 5 Effects of altered precipitation variability, application of fertilizer, and their interactive effects on soil nutrients nitrate (NO_3^-), ammonium (NH_4^+), potassium (K), phosphorus (P) (all in mg l^{-1}), total carbon (C), and nitrogen (N) (both in %); given are mean and standard errors (SE) of soil nutrients in precipitation variability treatments low, medium and $high_{early}$, and F and p- value of linear mixed effect models; significant effects ($p<0.05$) are in bold

	Precipitation variability						**Precipitation Variability**		**Fertilizer**		**Precipitation Variability X Fertilizer**	
	Low		Medium		$High_{early}$							
	mean	error	mean	error	mean	error	F	p	F	p	F	p
NO_3^-	1.18	0.13	1.10	0.11	**0.80**	**0.09**	4.59	**0.015**[1]	0.96	0.333	0.81	0.453
'NH_4^+	5.21	0.34	4.89	0.24	**4.06**	**0.15**	6.73	**0.003**[1.3]	0.90	0.348	0.73	0.490
K	7.92	0.37	9.11	0.44	**9.71**	**0.65**	4.76	**0.013**[2]	1.68	0.202	0.21	0.814
P	1.39	0.10	1.74	0.10	**1.86**	**0.13**	9.42	**0.000**[2]	10.13	**0.003***	0.18	0.832
C	2.34	0.06	2.39	0.09	2.30	0.10	0.37	0.692	2.36	0.131	0.60	0.556
N	0.20	0.01	0.20	0.01	0.20	0.01	0.41	0.666	1.99	0.165	0.48	0.625

'log transformed. *increased. [1] decrease by $highVar_{early}$ compared to lowVar. [2]increase by $highVar_{early}$ compared to lowVar. [3] decrease by $highVar_{early}$ compared to medVar

3.7. Influence of timing of extreme drought events on grassland in interaction with fertilizer or delay of harvest

Fertilizer raised crude protein content in the $highVar_{early}$ treatment, but not in the $highVar_{late}$ treatment (Fig. S1, interaction: precipitation variability X fertilizer: $F = 16.15$, $p = 0.0002$). There was no significant interaction between the timing of the drought in the high precipitation variability treatments and fertilization with respect to the productivity or other studied nutritive values of this grassland.

The 10-day delay of harvest did not alter the in vitro gas production in the $highVar_{early}$ treatment ($p = 0.8870$, Fig. S2). However, the grassland which experienced high precipitation variability including extreme drought and heavy rainfall events in summer ($highVar_{late}$) showed a decrease in in vitro gas production when harvested 10 days after the events ($p = 0.0016$, interaction: precipitation variability X delay of harvest: $F = 13.5$, $p = 0.0005$).

4. Discussion

Climate change is projected to increase the intra-annual precipitation variability, resulting in more extreme drought and heavy rainfall events. Our results show that grassland yield and composition as well as its forage quality are affected by alterations of intra-annual precipitation variability. We show that fertilization can buffer losses of forage yield due to high precipitation variability without a harvest delay although it cannot change the direction of response to altered precipitation variability. We demonstrate that increased intra-annual precipitation variability increased forage quality and thus compensation effects of fertilization and delayed harvest on forage quality were not as evident. A nitrogen dilution effect might have masked possible negative effects of precipitation variability on plant nitrogen. Furthermore, the response of forage quality to the tested management strategy under high intra-annual precipitation variability seemed to depend on the seasonal coincidence of the extreme weather events with plant maturity.

4.1. Effects of altered precipitation variability on forage yield and root length of grassland

Increased intra-annual precipitation variability decreased total forage yield of the studied grassland by ~19% (low - high) and changed the proportions of functional group biomass. The reduction of grass and increase of forb yields suggest a change in the community composition. Our finding of a decrease in total forage yield is comparable to findings of Fay et al. (2011) who showed that by increasing intra-annual rainfall variability aboveground yield was reduced in native tall-grass prairie. However, the effects of modified precipitation variability on yield in other studies indicate the importance of the type of grassland under climate change. Less variable intra-annual rainfall pattern with fewer but larger rainfall events was found to reduce the aboveground net primary productivity of a North-American mesic grassland (tallgrass prairie) but increased the yield of semi-arid grassland (Heisler-White et al. 2008, 2009). Root length did not respond to precipitation variability in our study. However, Walter et al. (2012) found a reduction of root growth under high precipitation variability compared to medium variability. Conversely, drought did not affect belowground biomass production of a grassland in a study by Gilgen & Buchmann (2009). An expected adaptation

to drought by stimulated root growth with increasing aridity as was found in several studies (Field et al. 1992; Kalapos et al. 1996; Kahmen et al. 2005; van Wijk 2011) could not be found in this study.

4.2. Effects of altered precipitation variability on forage quality of grassland

Increased intra-annual precipitation variability enhanced forage quality of the grassland. In general, the Relative Feed Value showed an increase in quality from low to medium and high variability. An increase of forage quality was also indicated by higher crude protein content and lower fiber content (crude fiber, NDF, ADF) with increasing precipitation variability. We expected a reduction of plant nitrogen content and crude protein (Buxton 1996; Durand et al. 2010) due to the applied drought event within the extreme precipitation variability treatment ($highVar_{early}$). We found the lowest protein content in the lowVar characterized by no water stress and continuous water availability. According to Buxton (1996) a moderate water stress can slow down grassland maturation, thereby maintaining crude protein content. However, soil moisture content in 2011 close to the permanent wilting point, high coefficient of variations of precipitation and soil moisture, and the decrease in forage yield imply that the drought was severe. We have to consider that the low protein content in lowVar and its increase with precipitation variability was very likely affected by nitrogen dilution (Lemaire & Gastal 1997). Lemaire & Gastal (1997) showed that plant nitrogen declined with increasing plant mass due to the ontogenetic decline of ratio of metabolic (high N content) versus structural (low N content) tissue with increasing plant size. An earlier study on drought effects on nitrogen contents in lucerne demonstrated that the negative effect of drought on N nutrition processes was nearly compensated by a positive effect due a lower dilution of N (Lemaire et al. 1989). Thus, the observed increase in forage quality with increasing precipitation variability might be partly misleading. However, crude protein was not increasing proportionally as biomass decreased with greater precipitation variability. The different functional groups show varying alterations in their yield (highest legume yield in medVar, increasing forb yield). The stability in nutritive value across the precipitation variability treatments might therefore been caused also by the change in functional community composition from grasses to forbs. Grasses are known to have higher NDF and lower crude protein contents than legumes (Buxton 1996; Hopkins & Wilkins 2006; Sanderson 2010). Furthermore, forb species feature lower NDF contents, higher feed values and higher digestibility compared to grasses (Bruinenberg et al. 2002; Duru et al. 2008). The reason why in vitro gas production of the forage did not respond to modified precipitation variability is probably because sugar content was not altered and the decrease in fiber contents was only small (Firkins et al. 1998; Hummel et al. 2006). According to the extrapolation of the N dilution concept to plant digestibility, there should be an increase of digestibility under water stress situations as in the highVar treatment (Lemaire et al. 1989; Lemaire & Allirand 1993). Our index for digestibility – in vitro gas production – was not affected by precipitation variability. However, the reduced NDF could partly indicate an increase of the metabolic to structural tissue ratio and thus better plant digestibility. The content of crude protein, ranging from 83 g kg-1 DM in the low precipitation variability treatment (lowVar) to 94 g kg-1 DM in the medium precipitation variability treatment (medVar) was lower than the world wide average crude protein content of 130 g kg-1 DM for grassland vegetation dominated by cold-season grasses (Buxton 1996) and lower than the comparable regional average of 133 g kg-1 for twice mown grassland (data from LfL Bayern). Further, the Relative Feed Value (RFV)

of our grassland was 85. According to the definition of RFV, values below 100 indicate low quality, values above 100 high quality of forage (Collins & Fritz 2003). Thus, crude protein and RFV indicate that the biomass in this study from all precipitation variability treatments was of low quality when given as forage for cattle.

4.3. Effects of altered precipitation variability and fertilization on soil nutrient status

We analyzed the soil nutrient status to reveal hidden effects of the precipitation treatments and the effectiveness of the fertilizer treatment. The drought period of the high precipitation variability treatment ($highVar_{early}$) resulted in the reduction of ammonium and nitrate in the upper soil layer probably due to decreased mineralization rates and microbial activity (Borken & Matzner 2009). Rewetting after drought leads to high microbial activity and high carbon and nitrogen fluxes within a very short time (Fierer & Schimel 2003; Borken & Matzner 2009). Content of potassium and phosphorus in the upper soil layer significantly increased with higher precipitation variability ($highVar_{early}$) probably due to decreased uptake by plants as was also shown for wheat by Nawaz et al. (2012). Root hairs and the release of root exudates are important for phosphorus uptake by plants (Brown et al. 2012). Although potassium can increase root hair growth under low moisture conditions, severe water stress inhibits and damages growth of root hairs (Sangakkara et al. 1996; Ma et al. 2010).

Application of fertilizer did not increase plant available nitrogen or potassium values in the soil, but additional nutrients could have been immediately taken in by plants, which was indicated by higher plant productivity after fertilization. Soil phosphorus content was increased by fertilization indicating incomplete phosphorus consumption by plants and therefore enrichment in soil. We conclude, that small amounts of granulate fertilizers entered the soil by solution during the drought event and were partly consumed by plants, the majority of fertilizer only reaching the soil after rewetting.

4.4. Buffering effects of fertilization and delayed harvest on forage yield against increased precipitation variability

We found no interactive effects between the harvest delay, fertilization, and increased precipitation variability on forage yield. Furthermore, fertilization during a drought period did not alter the direction of response of forage yield to extreme precipitation variability in this study. However, fertilization helped to keep grassland yield in the high precipitation variability treatment at the same level as the yield of unfertilized grassland under low precipitation variability. Thus, the application of fertilizer during the drought buffered the yield losses caused by increased precipitation variability. It should be considered that this was a short-term study and the alterations in forage yield by fertilization in interaction with increasing precipitation variability could change after several years, as changes in plant community composition continues. So far, we already discovered changes of the plant community composition by precipitation variability. An increase of the proportion of tall grasses with the application of fertilizer was found in a similar study by Cop et al. (2009b). However, nitrogen addition is known to alter community composition in long-term studies (Gough et al. 2000; Zavaleta et al. 2003). Therefore, future changes in the composition of the plant community by more variable precipitation patterns and fertilization could lead to opposing or additive effects on forage yield.

4.5. No buffering effects of fertilization and delayed harvest on forage quality against increased precipitation variability

We expected an interaction between altered precipitation variability with the application of fertilizer and a delayed harvest. Several days after the rewetting of the drought-exposed grassland should have provided sufficient time for the fertilizer granulate to dissolve and to improve the nutrient availability for plants. As a consequence, an increase in nutritive values especially crude protein could be expected to maintain forage quality. Indeed, fertilizer increased forage quality in terms of crude protein content in all precipitation variability treatments which is in accordance with other studies (Buxton 1996; Balabanli et al. 2010). However, additional time after the drought event was not required for the fertilizer to increase forage quality. We found also no interaction between the harvest delay and the increased precipitation variability for the tested parameters of forage quality. Similar to Buxton (1996), a decrease of crude protein by delayed harvest was found. However, the detected decrease by 8 g kg-1 was not as high as expected. The additional time for plant growth, stimulated by rewetting after the drought event, probably led to further lignification of plant material taking up energy and therefore reducing protein content. However, the decrease in forage quality by the delayed harvest was outweighed by the increased forage quality as a consequence of modified precipitation variability.

In general, we expected a decrease of forage quality by increasing precipitation variability, which should have been compensated by fertilization and delayed harvest. As forage quality was already increased by the altered precipitation pattern, compensation effects of fertilization and delayed harvest were not as evident.

4.6. Interactive effects of seasonality of extreme weather events and management strategy on forage quality

Additionally, we tested the influence of seasonal timing of the extreme weather events in interaction with the application of fertilizer and harvest delay on the forage quality. We examined the differences in responses to fertilization and harvest delay between the two high precipitation variability treatments. We found that the crude protein content of the grassland was increased by fertilizer at the end of the early drought event ($highVar_{early}$), but not at the end of the late drought event ($highVar_{late}$). This can be explained by the maturation of plants, including lower leaf/stem ratio and higher lignification of plant tissue until the time of the late high variability treatment. Another difference of the seasonality of the drought events in the high variability treatments was found in the response of in vitro gas production to the delayed harvest. The lower gas production, which indicated forage digestibility and energy content, was decreased by the delayed harvest only in the grassland that experienced a late drought and a heavy rainfall event. This can also be explained by the advanced plant maturity leading to a higher fiber content (Hummel et al. 2006). Thus, the response of forage quality to management tools applied by higher precipitation variability depends also on the timing of the extreme weather events.

4.7. Limitations and recommendations

We studied a low productive grassland, which is a common grassland system in the study area and therefore important to conserve with low management effort. We are aware that fertilizing this species-rich, low productivity grassland can lead to species losses (Suding et al. 2005). Fertilizer should be applied only in exceptional cases to reduce acute damages. We tested this management strategy mainly because it would not have to be applied in advance, but could be applied as soon as it becomes obvious that an extreme drought period takes place. The search of a management tool that is not cost-intensive and does not endanger species but which is easy applicable should therefore continue. Furthermore, the different responsiveness of studied nutritive values to the applied management tools – fertilization and delayed harvest – makes it difficult to recommend one single strategy. However, we see the main driver and crucial point for conservation of forage yield and quality in the shifts in plant community composition in terms of functional group proportion. Plant species, or even different plant ecotypes (plants of the same species but with different geographical origin and environmental conditioning, also referred to as provenances, i.e. adaptations; see Kreyling et al. (2011)) might be found which are not only resistant in their productivity against drought and heavy rainfall events but which are also of high forage quality. These kinds of species or varieties could proactively buffer negative effects of increased precipitation variability. However, introducing new species or ecotypes might imply the risk of unexpected changes such as unwanted competitive interactions between the new and resident species or substantial alterations of the current species composition which has to be ruled out before introduction. Nevertheless, conservation of biodiversity would offer a pool for the selection of species or within-species varieties with appropriate adaptations to altered precipitation patterns due to climate change.

Conclusion

Increased intra-annual precipitation variability decreased forage yield and increased forage quality of a temperate grassland via increased plant water stress. Alterations in the plant community composition and plant maturity stage as well as the nitrogen dilution with increasing plant growth were the main drivers of forage quality change. Application of fertilizer increased key nutritive values, especially crude protein, but was not influential in maintaining forage quality under high precipitation variability. Nonetheless, fertilization reduced losses in grassland annual yield that were induced by extreme precipitation variability. Delaying grassland harvest to enable fertilizer to increase soil nutrient availability and encourage fast recovery of plants was not an effective management strategy in the face of varied precipitation patterns. The timing of extreme weather events was a determining factor in the responsiveness of forage quality to the tested management strategies. Further strategies need to be developed which acknowledge a shift in plant species compositions as one of the main driver of changes in forage quality in the face of globally altered precipitation patterns.

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Supplementary Material Manuscript 2

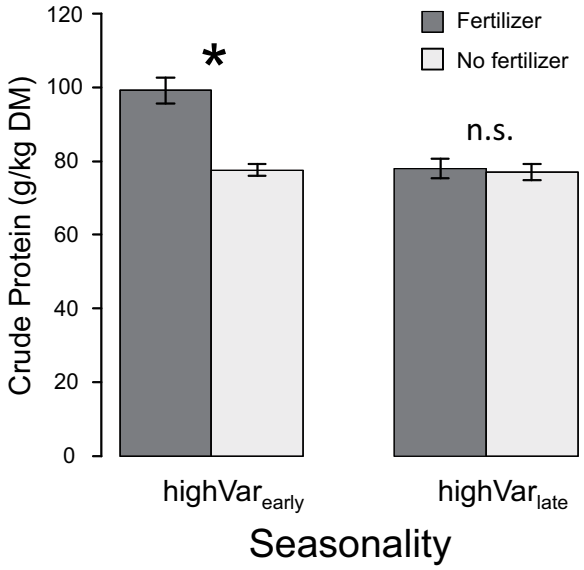

Figure S1 Effect of fertilizer application on crude protein content in grassland under high precipitation variability depends on timing of extreme weather events; given are mean values and standard errors for fertilized (dark grey) and not fertilized (light grey) grassland communities, asterisk indicates significant and n.s. no alterations in crude protein content by fertilization ($p<0.05$)

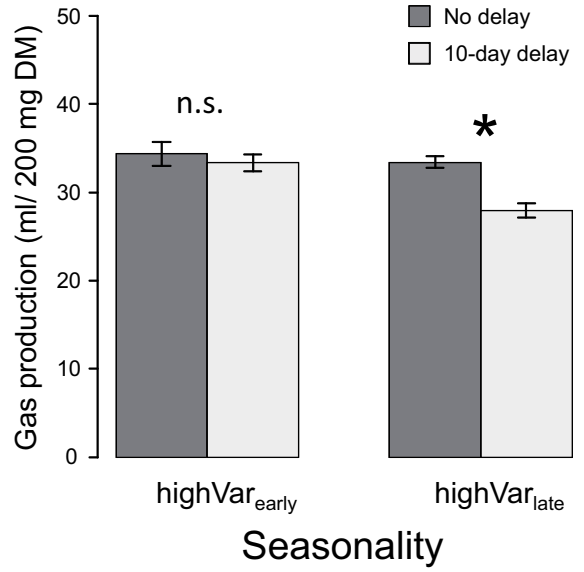

Figure S2 Effect of 10-day delay of harvest on in vitro gas production in grassland under high precipitation variability depends on timing of extreme weather events; given are mean values and standard errors for non-delayed (dark grey) and 10-day delayed (light grey) harvested grassland communities, asterisk indicates significant and n.s. no significant alterations in in vitro gas production by delay ($p<0.05$)

Manuscript 3

Increased rainfall variability reduces biomass and forage quality of temperate grassland largely independent of mowing frequency

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Increased rainfall variability reduces biomass and forage quality of temperate grassland largely independent of mowing frequency

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Abstract

Climate models indicate that global warming will stimulate atmospheric exchange processes and increase rainfall variability, leading to longer dry periods and more intense rainfall events. Recent studies suggest that both the magnitude of the rainfall events and their frequency may be as important for temperate grassland productivity as the annual sum. However, until now interactive effects between land management practice, such as mowing frequency, and rainfall variability on productivity and forage quality have not been studied in detail. Here, we present the data from a field experiment (EVENT II) in which a Central-European grassland was subjected to increased spring rainfall variability (low, intermediate and extreme rainfall variability without any change to the rainfall amount) and increased mowing frequency (four times compared to twice a year).We assessed biomass production, forage quality parameters, root- length and shoot–root ratio. Enhanced spring rainfall variability reduced midsummer productivity and the leaf N and protein concentrations of a target species, but did not exert any long-term effects on biomass production and forage quality in late summer. However, the increased spring rainfall variability reduced aboveground net primary productivity by 15%. More frequent mowing increased productivity in the first year of the study, but decreased productivity at the end of the second year, showing a decline in the potential for overcompensation after a history of more intense mowing. Generally, more frequent mowing decreased the shoot–root ratio and increased the concentration of leaf N. Increased mowing frequency neither buffered, nor amplified the adverse effects of rainfall variability on productivity, but made leaf N concentrations in early summer more responsive to altered rainfall patterns. These results highlight the fact that even relatively small and short-term alterations to rainfall distribution can reduce production and forage quality, with little buffering capacity of altered mowing frequency. Comparisons with productivity data from the first year of the study, in which both, rainfall distribution and rainfall amount were modified, demonstrate the crucial role of sufficient moisture (annual rainfall amount) for grassland resilience: in this first year, negative effects of extreme rainfall variability lasted until the end of the year. To conclude, increased rainfall variability under climate change will likely affect agricultural yield in temperate meadows. Management strategies to buffer these effects have yet to be developed.

Keywords: EVENT II experiment, Extreme weather event, Rainout-shelter, Forage quality, *Alopecurus pratensis, Trifolium pratense*

1. Introduction

Climate change is projected to modify not only annual precipitation sum, but also to result in more extreme rainfall regimes in many parts of the world (IPCC 2007; Jentsch & Beierkuhnlein 2008). This will cause more severe drought periods as well as an increase in the frequency and magnitude of extreme precipitation events (Trenberth et al. 2003; Min et al. 2011). Evidence is mounting that the frequency and severity of droughts and extreme precipitation events has already increased over recent decades in many regions (Blenkinsop &Fowler 2007; Haylock & Goodess, 2004; IPCC 2007). Primary productivity and ecosystem functioning in terrestrial ecosystems are strongly influenced by the annual amount of precipitation (Sala et al. 1988). However, recent research suggests that rainfall variability may exert an even stronger influence on ecosystem functioning, where especially temperate grassland systems seem to be responsive to changes in rainfall variability. In grassland, more extreme rainfall regimes (less, but more intense rainfall events) affect ANPP (aboveground net primary productivity) (Barrett et al. 2002; Fay 2009; Heisler-White et al. 2009; Knapp et al. 2002), carbon cycling (Chou et al. 2008; Fay 2009; Harper et al. 2005) and N mineralization (Barrett et al. 2002; Heisler-White et al. 2009). The latter may in turn affect leaf quality in terms of N or protein content. Large reductions in ANPP have been shown in mesic grassland in response to more extreme rainfall patterns (Fay et al. 2003; Heisler-White et al. 2009; Knapp et al. 2008). In addition to the rainfall amount and variability, land management strategies, such as mowing frequency, can affect productivity and leaf litter quality in managed grassland. More frequent cutting is known to increase leaf N content. However, whether or not mowing increases or decreases the productivity of grassland depends on the mowing intensity, e.g. mowing history, mowing frequency and cutting height (Green & Detling 2000; McNaughton 1979; Turner et al. 1993; Weigelt et al. 2009). Mowing or defoliation is likely to alter the response to rainfall variability by altering plant community composition (Swemmer & Knapp 2008). Furthermore, a reduction of transpirative tissue alters water uptake and consumption and therefore reaction toward rainfall (Heitschmidt et al. 1999; McNaughton 1979; Yang & Midmore 2004). Currently, a knowledge gap exists on how land management practices, such as mowing frequency, are interacting with more extreme rainfall regimes: increased mowing frequency might buffer the effects of rainfall variability on grassland, diminishing the amplitude of the response toward rainfall extremes (Swemmer & Knapp 2008). A study by Bernhardt-Römermann et al. (2011) indicates that climate parameters get less important for biomass production under intermediate mowing frequencies. However, land management strategies might also amplify the effects of rainfall variability. To our knowledge, this is the first study to experimentally manipulate mowing and rainfall patterns in European managed grassland (meadows) in order to identify any potential interactions between rainfall variability and mowing frequency. The primary objectives of our study were (1) to investigate the factorially combined effects of increased spring rainfall variability and increased mowing frequency on the productivity and the forage quality of semi-natural, Central-European temperate grassland and (2) to determine, whether mowing frequency amplifies or buffers the effects of rainfall variability on biomass production and leaf quality of a target species. We conducted a field experiment in which we altered the temporal distribution and the magnitude of the rainfall events, but not

the overall rainfall sum. To assess potential interactions between rainfall variability and mowing frequency, we crossed the factor rainfall variability with the factor mowing frequency (two or four times per year). In the previous year, we altered the total rainfall amounts along with the alterations in rainfall variability. This enables a comparison between the effects of the altered total rainfall amounts and distribution and the effects of altered rainfall variability under constant total rainfall amounts. We hypothesized that

(I) increased rainfall variability negatively affects productivity and leaf quality, as has been shown for other mesic grasslands,

(II) increased rainfall variability alone can cause changes in productivity that are comparable to changes caused by alterations in both, variability and the annual sum of rainfall together,

(III) more frequent mowing increases productivity and forage quality, as has been shown for more frequent, but still moderate mowing frequencies,

(IV) more frequent mowing buffers adverse effects of increased rainfall variability on productivity and leaf quality, as growth responses might be synchronized and less responsive to rainfall changes after mowing.

2. Materials and methods

2.1. Study site

The study was conducted within the EVENT II experiment in a semi-natural grassland in the Ecological Botanical Garden of the University of Bayreuth, Germany, Central Europe (49°55'19''N, 11°34'55''E, 365 m asl) (Jentsch & Beierkuhnlein 2010). Communities are dominated by tall grasses, especially *Alopecurus pratensis* L. (meadow foxtail). The regional climate is temperate and moderately continental, with a mean annual temperature of 8.2 ◦C (1971–2000),and daily means ranging between −19.6 and 27.6. The mean annual precipitation of 724 mm (1971–2000) has a bimodal distribution with a major peak in June/July and a second peak in December/January (data: German Weather Service). The experiment was installed on a semi-natural, established meadow. For more than 20 years prior to the experiment, the meadow was mown twice per year and not fertilized. The rectangularly shaped experimental area has a total height difference of 95cm within the diagonal from southwest to north east, and about 7cm from southeast to north west. The soil of the experiment is classified as Stagnosol with a sandy-loamy Ap-horizon of about 30cm depth, a strongly loamy Sw-horizon (20cm) and a sandy-clayey Sd-horizon (>40 cm). Plant roots mainly occur in the upper 15cm, with almost no roots penetrating below the A-horizon, mean pH-value is 5.9.

2.2. Experimental design

The EVENT II experiment was established in 2008. The experimental design consists of two factorially crossed factors: (1) manipulation of the temporal distribution and magnitude of rainfall events in the growing season and (2) manipulation of mowing frequency. We implemented three scenarios of rainfall variability treatments in 2008 and 2009, assigned to the same plots: (1) low rainfall variability with weekly irrigation, ensuring a continuous water supply, (2) intermediate rainfall variability, with natural ambient rainfall variability and (3)

extreme rainfall variability, including an extreme spring drought. In 2008, the first year of the study, total growing season amount of rainfall and variability of rainfall were altered. This made it possible to assess direct drought effects, as the extreme rainfall variability treatment also received least total rainfall (see Table 1 for an overview over soil moisture and rainfall parameters in both years).

Table 1 Average soil moisture [vol %], variation coefficient (CV) of soil moisture [%], number of rainfall events exceeding 1 mm, the sum of the rainfall amount [mm] and the variation coefficient (CV) of daily rainfall amount [%] in 2008 and 2009.

			Treatment			
Parameter[1]	**year**	**time span[2]**	**low**	**mid**	**extreme**	**natural**
average soil moisture	2008	26/05-30/10 2008 (158 days)	**29**	21	19	
	2009	01/04-31/10 2009 (214 days)	**30**	29	25	
	2009	01/04-17/05 2009 (47 days)	**42**	40	36	
	2009	-29/06 2009 (43 days)	**29**	**29**	21	
	2009	-09/08 2009 (43 days)	**32**	31	27	
	2009	-28/10 2009 (80 days)	23	**24**	22	
CV soil moisture	2008	26/05-30/10 2008 (158 days)	20	31	**38**	
	2009	01/04-31/10 2009 (214 days)	35	35	**37**	
	2009	01/04-17/05 2009 (47 days)	6	8	**13**	
	2009	-29/06 2009 (43 days)	21	24	**30**	
	2009	-09/08 2009 (43 days)	25	**29**	26	
	2009	-28/10 2009 (80 days)	35	**36**	35	
no. of events	2008	26/05-30/10 2008 (158 days)	**61**	53	45	
	2009	01/04-31/10 2009 (214 days)	**80**	71	60	
	2009	01/04-17/05 2009 (47 days)	**19**	16	16	
	2009	-29/06 2009 (43 days)	**17**	13	1	
	2009	-09/08 2009 (43 days)	**17**	16	**17**	
	2009	-28/10 2009 (80 days)	**27**	25	25	
precipitation sum	2008	26/05-30/10 2008 (158 days)	**445**	335	296	335
	2009	01/04-31/10 2009 (214 days)	597	597	597	459
	2009	01/04-17/05 2009 (47 days)	**130**	100	100	100
	2009	-29/06 2009 (43 days)	103	**108**	37	77
	2009	-09/08 2009 (43 days)	164	152	**224**	127
	2009	-28/10 2009 (80 days)	200	**205**	**205**	155
CV precipitation	2008	26/05-30/10 2008 (158 days)	164	183	**204**	183
	2009	01/04-31/10 2009 (214 days)	204	256	**297**	227
	2009	01/04-17/05 2009 (47 days)	227	**280**	**280**	**280**
	2009	-29/06 2009 (43 days)	156	248	**656**	183
	2009	-09/08 2009 (43 days)	192	205	**223**	220
	2009	-28/10 2009 (80 days)	203	**275**	**275**	192

[1] Highest values in each category are in bold.
[2] Values for the vegetation period 2008 and 2009 and for the time spans between the compensation irrigation treatments in 2009 for the differing rainfall variability treatments are given. Values for 2009 shown over one time span begin with a compensation irrigation and exclude the following compensation irrigation, as the latter is only effective for soil moisture and biomass for the following period.

In 2009, the main year of the study, we controlled the amount of rainfall over the growing season for all treatments and manipulated only the distribution of rainfall, in order to isolate the effect of rainfall variability. All rainfall variability treatments were adjusted to the total 597mm of rainfall of the low variability treatment in four compensation irrigations (Table 2). Thus, not only the length of the dry intervals, but also the magnitude of rainfall per event was changed. The low rainfall variability treatment received at least the 30-year weekly average rainfall each week. The vegetation periods from 1971 to 2000 served as a reference (data:

German Weather Service). Missing amounts on natural rainfall were added if the weekly rainfall was less than the long-term average for the same week. This treatment ensured continuous water availability. If weekly rainfall exceeded the long-term sum, it was not subtracted for the next irrigation. For 2008, the overall rainfall amount of 553 mm on the low rainfall variability treatment (natural plus irrigated rainfall) within the vegetation period (April 1st–October 30th) exceeded the 30-year-average by 94 mm. In 2009, the total amount of 597 mm, irrigated on all treatments by applying compensation irrigations (see below), exceeded the 30-year-average by 138 mm. Both years consequently resemble rather wet years. The intermediate rainfall variability treatment remained under ambient conditions without any treatment, except for the compensation irrigations applied in 2009 which adjusted rainfall sum to the low rainfall variability treatment at four points of time (Table 2). Thus, in 2009 the intermediate rainfall variability treatment received the ambient rainfall plus the compensation irrigations. In the extreme variability treatment, rainout shelters excluded natural rainfall in the early growing season for 42 days from May 19th until June 30th in both years, resulting in an extreme spring drought. The tunnel shaped rainout shelters had a base area of 5.5 m by 7.5 m and a height of 2.5 m. A metal frame was covered by low- density polyethylene foil which allowed a nearly 90% penetration of photosynthetically active radiation. The foil started from a height of 80 cm off the ground to allow near-surface air-exchange, thus reducing any microclimatic artefacts, like increased temperatures or reduced wind speed. The rainout shelters have a buffer zone of 1 m around the plots toward the shelter edge and additional plastic sheet pilings around the treatment within the buffer zone reaching down to a depth of 25 cm avoiding rain run-off to flow into the treatment. Due to the compensation irrigation, the extreme spring drought was followed by 2 days of heavy rainfall in 2009. Such a scenario resembles future projections of drier growing seasons with more extreme rainfall events for Germany (Jonas 2005; Jacob 2009). We installed an additional roof-artefact control during the spring drought manipulation of the extreme variability treatment where natural rainfall was applied under rainout shelters, resembling the rainfall of the intermediate rainfall variability treatment. We did not observe any differences in biomass production between the roof-artefact control and the intermediate variability treatment. Irrigation was applied using portable irrigation systems (Kreyling et al. 2008b). A lateral surface flow was reduced using plastic sheet pilings around all plots reaching down to a depth of 20–25cm.

Table 2 Amount and timing of compensation irrigation [mm] in 2009 on the extreme and intermediate rainfall variability treatments given to apply the same overall rainfall amount on all treatments over the vegetation period.

	treatment	
date	extreme	mid
May 18th	36.6	36.6
June 30th	96.5[1]	25.1
August 10th	60.3	60.3
October 28th	32	32

[1]applied on two consecutive days

To determine the interactions between rainfall variability and mowing frequency, two different mowing frequencies were applied and nested within the rainfall variability treatment, thus resulting in a split-plot design (with rainfall variability manipulation being the plot factor, and mowing frequency the subplot factor). Each rainfall manipulation block was split into four

plots with different mowing frequencies, each plot 1.5 m ×1.5 m in size: two plots per block were mown only twice per year and two plots were mown four times per year. Each rainfall variability manipulation block was replicated five times and was restricted to occur just once in each row and each column of the experimental design. Within one rainfall manipulation block, mowing frequency plots were 50 cm apart from each other, the rainfall manipulation blocks were located 3 m apart from each other.

2.3. Soil moisture

Soil moisture was logged every hour using frequency domain (FD)-sensors (ECH2O, Decagon devices, Pullman, USA) that had been installed in May 2008 in each plot to capture the dynamics of soil water content in response to rainfall variability (n=5/treatment). Each sensor measured the soil moisture between −2 and −7 cm. According to the root length data, the majority of root biomass is located within the upper 5 cm of the soil. Average daily values were calculated for analysis.

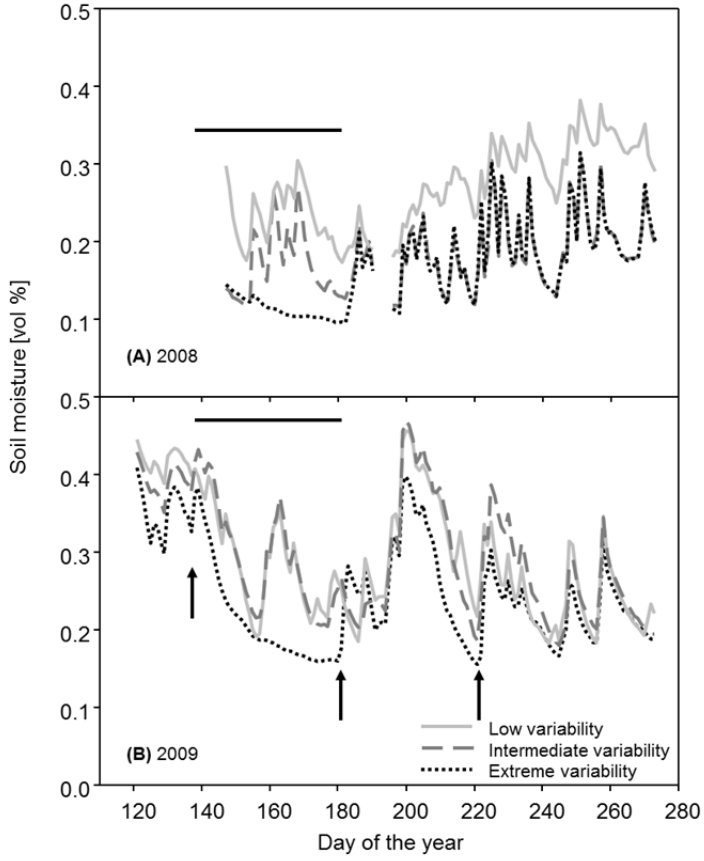

Figure 1 Soil moisture response to (A) altered rainfall variability and altered rainfall sum (2008) and (B) to altered rainfall variability with constant rainfall sum (2009). Results for low rainfall variability (light grey solid line), intermediate rainfall variability (dark grey dashed line) and extreme rainfall variability (black dotted line) are shown throughout the vegetation period. In 2008, measurements started on May 26th (day 147 of the year) and results are missing from July 9th until July 13th (days 191-195 of the year) due to a technical error. The black vertical line indicates the length of the drought for the extreme variability treatment (days 138-181 of the year), the black arrows indicate the timing of the first three compensation irrigations in 2009 (amounts of irrigation for each weather treatment given in Table 1). Soil moisture was recorded at a depth of -2 - -7 cm using FD sensors.

2.4. Biomass production and ANPP

Primary productivity was estimated based on the total above-ground harvest of all plant material in two 0.1 m^2 rectangles from the core of each plot. Harvesting was conducted in the first week of July and in the second week of September for the plots that were mown twice per year. The plots that were mown four times per year had additional harvests in the third week of May and the first week of August. To compare the results of productivity for July and September, the weight of aboveground dry biomass was summed for the plots that were already mown before (the cumulated biomass of May and July for the July harvest and the cumulated biomass of August and September for the September harvest for the plots mown four times per year). The dry weight of the two rectangles was averaged. To assess ANPP, the total biomass produced over the whole year was calculated. Aboveground biomass was dried at 70°C for 72h and weighed to the nearest 0.1 g.

2.5. Root length and shoot–root ratio

Root length was acquired by the minirhizotron technique in 2009. One clear plastic tube (5 cm in diameter) was installed at a depth of 45 cm at a 45° angle at the beginning of 2009. Images of 3.8 cm^2 were taken at 5 cm, 15 cm, 25 cm, and 35 cm depth along each tube by a digital camera mounted on an endoscope. The images in each plot were taken in the week after the first drought period (July 1st–July 4th) and at the end of the vegetation period (September 14th–September 18th). Images were analyzed for root length using the line intersection method (Tennant 1975) within a systematic grid (10×10, grid width of 0.2 cm × 0.2 cm). Afterwards, the values for each depth were summed to assess the summed root length over all rooting depths. Shoot–root ratio was evaluated using the ratio between above-ground biomass and the summed root length over all depths (Kreyling et al. 2008a). Both parameters were standardized beforehand to the same mean and standard deviation due to the different measured units of above- and belowground parameter.

2.6. Forage quality

To determine leaf N (N) and carbon (C) concentrations of the dominant tallgrass, *A. pratensis*, one mixed sample per plot was taken after drying and weighing the biomass in 2009. Samples were ground in a ball mill and analyzed with an elemental analyser (Thermo Quest Flash EA 1112). To provide additional information about the impacts of drought on the forage quality in other species, we include data from another sampling campaign here. In this, we assessed the drought effects on the protein content of the key legume *Trifolium pratense*. We took mixed samples from the leaves of three different plants on the last day of the drought treatment, which were immediately frozen in liquid N. We determined the total soluble proteins according to Bradford (1976). Soluble proteins were extracted using 50 mM Tris–HCl (pH 7.6) and 1 µM PMSF.

2.7. Statistical analysis

We performed two-factorial ANOVA in order to test for the significance of the effects of the fixed factors rainfall variability treatment and mowing frequency on the response variables. To account for the split-plot design, we included the row and the column of the weather treatment blocks as random factors in our linear mixed effect model, as each rainfall manipulation was restricted to occur just once in each row and each column of the design. To include row and column number as random effects automatically implements the nesting of mowing frequency within rainfall treatment blocks in the model, as one weather treatment

block with its corresponding and unique row and column combination includes four values of the response variable (within one block the two mowing frequencies are represented twice each) (Faraway, 2006). Prior to analyses, we tested whether the assumptions of an ANOVA, homogeneity of variances and normally distributed errors had been met by visually checking the residuals against the fitted plots and the normal qq-plots (Faraway 2006). If these assumptions were not fulfilled then the data were square-root (root length) or log-transformed (biomass, N data). All statistical analyses were performed using R 2.11.0 (R Development Core Team 2010). For mixed effect models we used the software package lme4 (Bates & Maechler 2010), and the package multcomp (Hothorn et al. 2008) for multiple post hoc comparisons. Significance levels in mixed effect models were evaluated by Markov Chain Monte Carlo sampling of 1000 permutations, using the software package language R(Baayen, 2009).

3. Results

3.1. Rainfall and soil moisture characteristics

The vegetation period for the year 2008 (April 1st–October 31st) with a total sum of 427 mm of rainfall was slightly drier than the long-term average rainfall sum of 437 mm for the time period 1971–2000, whereas the vegetation period for 2009 was slightly wetter (459 mm). Fig. 1 shows soil moisture dynamics for 2008 and 2009. In 2008, the overall soil moisture from May 26th until the end of October was greatest and least variable (expressed as CV: coefficient of variation: standard deviation/mean) in the low rainfall variability treatment, followed by the intermediate and then the extreme rainfall variability treatment. Variability of total daily rainfall was most variable in the extreme variability treatment and least variable in the low variability treatment (Table 1). The rainfall treatments in 2009 caused changes in soil water dynamics in terms of soil moisture and variability in soil moisture (Table 1). Mean soil moisture over the whole vegetation period for medium rainfall variability and low rainfall variability did not greatly differ (difference <4%), but was reduced by around 17% in the extreme rainfall variability treatment compared to the low rainfall variability treatment. In each of the four periods between compensation irrigation, soil moisture was lowest for the most extreme rainfall variability treatment, particularly during the drought period, where it was reduced by 28% compared to the other two treatments. Variability in soil moisture (CV) in each of the four periods was lowest for the low rainfall variability treatment, although the overall annual CV was almost the same in the intermediate rainfall variability treatment (difference <0.5%). Variability in soil moisture and daily rainfall amount was overall greatest in the extreme rainfall variability treatment (Table 1).

3.2. Effects of increased rainfall variability, modified rainfall amounts and mowing frequency in 2008

In 2008, diminished rainfall amounts and increased rainfall variability negatively affected biomass production in July (in the following, we give degrees of freedom (df) and residual df in parentheses after F in the following notation: F(df, residual df)). ($F(2,56)=3.44$; $p=0.039$) and September ($F(2,56)=22.05$; $p<0.001$), as well as ANPP ($F(2,56)=13.52$; $p<0.001$) (Fig. 2a–c). In July, biomass production was reduced by 21% in the spring drought treatment (extreme variability) compared to the low rainfall variability treatment with the overall highest rainfall amounts ($p=0.025$) (Fig. 2a). In September, biomass production was reduced by 49% in the extreme variability treatment with the overall lowest rainfall sum and by 35% under ambient rainfall compared to the low variability treatment that was regularly watered

(p<0.001), with marginally significant differences between the intermediate and extreme variability treatments (p=0.087) (Fig. 2b). Overall ANPP was lowered by 33% in the extreme variability treatment and by 17% in the intermediate variability treatment compared to the low variability treatment (p<0.001 and p=0.031). ANPP in the extreme variability treatment with the lowest rainfall amounts was lowered by 19% compared to the intermediate variability treatment (p=0.021) (Fig. 2c). More frequent mowing generally increased biomass production in July 2008 (F(1,56)=5.70; p=0.02) (Fig. 2d) and September 2008 (F(1,56)=5.99; p=0.018) (Fig. 2e), and thus increased ANPP in 2008 (F(1,56)=4.23; p=0.044) (Fig. 2f). There were no significant interactions between mowing frequency and rainfall variability in 2008 (data not shown).

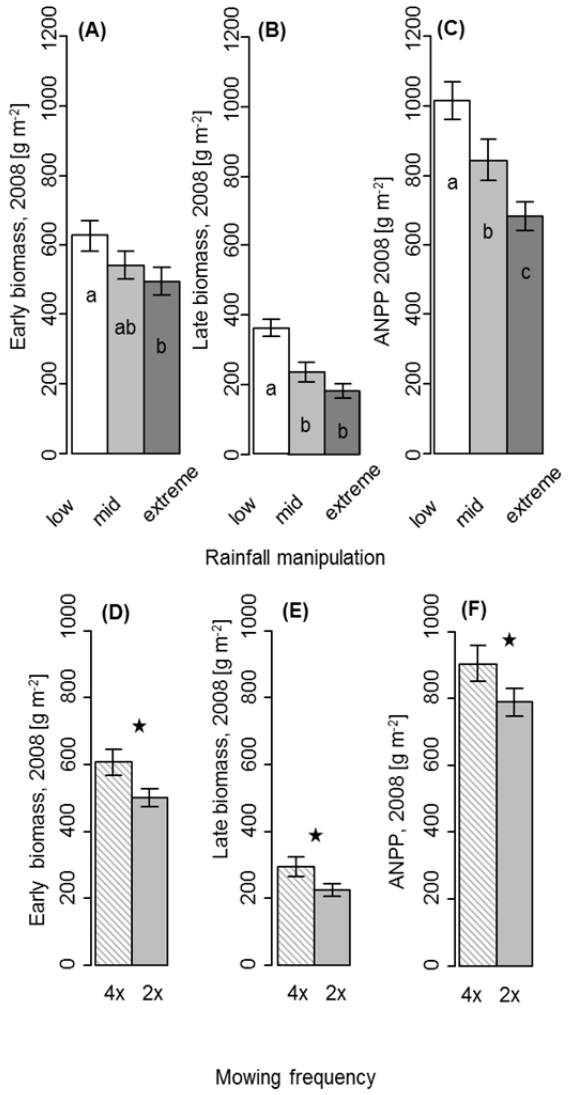

Figure 2 Effects of altered rainfall variability and rainfall sum (A-C) and of altered mowing frequency (D-F) in 2008. Biomass production in (A) July 2008, (B) September 2008 and (C) ANPP in 2008 in response to altered rainfall variability and rainfall sum and in response to altered mowing frequency (D-F, patterned bars: mown four times per year, shades bars: mown twice per year). In graphs A-C, white bars show the low variability treatment with the highest overall rainfall amounts, light grey bars show the intermediate variability treatment with intermediate rainfall amounts, and dark grey bars show the extreme variability treatment with the lowest overall rainfall amount. Means ±1SE are shown, different letters and asterisks indicate significant differences below p=0.05.

3.3. Effects of increased rainfall variability in 2009

Rainfall variability significantly altered biomass production in the early summer of 2009 (F(2,56)=11.19; p<0.001), shortly after extreme drought followed by heavy rainfall was applied to the extreme variability treatments (first week of July) (Fig. 3a) . Communities subjected to the extreme rainfall variability revealed 20% less aboveground biomass compared to the low variability treatment (p<0.001) and 13% less biomass compared to the intermediate variability treatment (p=0.002). These strong effects of extreme rainfall

variability assessed in July did not persist until September, as then extreme rainfall variability did not significantly affect biomass production ($F(2,56)=0.72$; $p=0.49$) (Fig. 3b). Nevertheless, the strong early summer effects of extreme rainfall variability led to negative ANPP responses ($F(2,56)=9.11$; $p<0.001$), as communities under extreme rainfall variability produced 15% less biomass than communities under low variability treatment ($p<0.001$) and 7% less biomass than communities under intermediate variability treatment ($p=0.024$) (Fig. 3c). A redistribution of rainfall resulted in changes in the summed root length in July ($F(2,56)=4.41$; $p=0.017$) (Fig. 3d). The summed root length was highest in the intermediate rainfall variability treatment and 43% and 24% shorter in extreme and low rainfall variability treatments ($p=0.024$ and $p=0.032$, respectively). In September, no differences occurred in the summed root length ($F(2,56)=2.17$; $p=0.12$) (Fig. 3e). The shoot–root ratio in July was affected by extreme rainfall variability ($F(2,56)=5.44$; $p=0.007$), as it was increased by 22% in the low rainfall variability treatment when compared to the intermediate rainfall variability treatment ($p=0.003$) (Fig. 3f). The effect of this rainfall variability treatment on shoot–root ratio persisted until September ($F(2,56)=4.10$; $p=0.022$), as the shoot–root ratio was still increased in the low rainfall variability treatment compared to the intermediate rainfall variability treatment ($p=0.017$) (Fig. 3g). Increased spring variability in rainfall patterns also affected the forage quality in early summer: leaf N concentration of the target grass A. pratensis was decreased in July under extreme rainfall variability compared to low ($p<0.001$) and intermediate rainfall variability treatments ($p=0.037$; overall rainfall treatment effect $F(2,54)=5.03$; $p=0.01$) (Fig. 3h). The C/N ratio in June was marginally significantly affected by rainfall variability ($F(2,54)=3.07$;$p=0.055$), as it was increased under extreme rainfall variability compared to low rainfall variability ($p=0.002$) (Fig. 3j). Rainfall effects on N concentration and C/N ratio interacted with effects of mowing frequency, shown in Section 3.5. Extreme rainfall variability did not affect the forage quality in September, as neither leaf N concentration ($F(2,56)=1.71$; $p=0.19$) nor the C/N ratio ($F(2,56)=1.19$; $p=0.31$) in *A pratensis* was altered in response to rainfall treatments (Fig. 3i and k). Protein content in the legume *T. pratense* was also affected by rainfall variability treatments ($F(2,54)=12.33$; $p<0.001$), as protein content was increased under a low rainfall variability treatment when compared to intermediate and extreme rainfall variability ($p<0.001$) (Fig. 3l).

3.4. Effects of the mowing frequency in 2009

In 2009, more frequent mowing caused a marginally significant positive response of productivity during midsummer: the cumulated biomass of the two harvests until July 2009 in the communities that had been mown four times was 12% greater than the biomass production in those plots that had only been mown twice per year ($F(1,56)=11.19$; $p=0.057$) (Fig. 3a). Contrastingly, more frequent mowing in mid and late summer resulted in a 32% decrease in biomass compared to those communities that had only been mown twice per year ($F(1,56)=38.66$; $p<0.001$) (Fig. 3b). This reversal of effects resulted in ANPP showing no response to altered mowing frequency over the whole year ($F(1,56)=2.00$; $p=0.16$) (Fig. 3c). The shoot–root ratio decreased consistently by more frequent mowing in early ($F(1,56)=58.79$; $p<0.001$) and late ($F(1,56)=21.04$; $p<0.001$) summer (Fig. 3f and g), whereas the root length was not affected at any point in time (Fig. 3d and e). The C/N ratio in leaves of *A. pratensis* in July decreased ($F(1,54)=122.02$; $p>0.001$) and N concentration increased ($F(1,54)=109.81$; $p<0.001$) as a result of more frequent mowing in early summer (Fig. 3h and j), both interacting with rainfall variability (see Section 3.5). The same effect of mowing frequency on the leaf N relation was observed in September ($F(1,56)=14.49$ for N content and 15.99 for C/N ratio; $p<0.001$) (Fig. 3i and k).

3.5. Interactions between rainfall variability and mowing frequency

Mowing frequency did not interact with rainfall variability in terms of productivity, root length or shoot–root ratio in any year. There was a significant interaction for leaf N concentration and consequently C/N ratio in July 2009 ($F(2,54)=5.34$; $p=0.011$ and $F(2,54)=3.54$; $p=0.036$, respectively): differences in N concentrations caused by rainfall variability were comparatively greater for more frequently mown communities (Fig. 3h), which caused the significant interaction between mowing frequency and rainfall variability. Accordingly, the differences in the C/N ratio in July caused by rainfall variability were comparatively greater in those plants that were mown more frequently and was hardly noticeable in plants mown only twice per year (Fig. 3j).

4. Discussion

Climate change is projected not only to alter the annual amount of rainfall, but also rainfall variability, resulting in more intense rainfall events and longer dry periods in between. Our results emphasize that overall rainfall amount is a strong driver of grassland productivity and forage quality. However, we demonstrate that this is not only caused by mere differences in amount, but also by differences in rainfall variability which usually accompany shifts in rainfall amounts: we show that altered rainfall variability even under constant rainfall amounts affected community productivity and also the leaf quality of our target species. Mowing frequency strongly affected biomass production and quality, but neither buffered nor amplified the effects of rainfall variability on productivity.

4.1. Effects of increased rainfall variability in 2009, compared to the effects of increased rainfall and modified rainfall amounts in 2008

In the dry year of 2008, soil moisture for the low variability treatment was always higher compared to the other two treatments, according to the highest total rainfall amount. The effects from the rainfall treatments (altered amount and variability) on productivity were generally greater in 2008 and lasted longer than in 2009. We did not expect such great effects in the first year of the study, as other studies often show weaker, lagged or even no effects of grassland productivity toward drought (Bloor et al. 2010; Gilgen & Buchmann 2009; Kreyling et al. 2008b). These results highlight the important role of the overall rainfall amount for grassland productivity. In 2008 there were also differences in biomass production between the low rainfall variability treatment with the highest rainfall amounts and the intermediate rainfall variability treatment with the lower rainfall amounts, whereas in 2009, when both treatments received the same amount of rainfall, there were no differences between the low and intermediate rainfall variability treatments. Nevertheless, the results from 2009 showed that changes in rainfall variability can only affect productivity, when the variability is extreme. However, we show that it is not only rainfall amount that influences productivity and forage quality of temperate grassland, but also the rainfall variability and intervals, in which a given rainfall amount is applied. The relatively short-lived effects of extreme spring rainfall variability in 2009, compared to the long-lasting effects of the treatments in 2008, highlight the importance of sufficient water availability and thus the total rainfall amounts for grassland resilience. Therefore, in contrast to the studies on mesic grassland systems of North America (Fay et al. 2003; Knapp et al. 2002), here, in temperate grassland of Central-Europe, overall rainfall amount seemed to influence ANPP stronger than rainfall variability alone. We cannot completely rule out the possibility that the drought effect of 2008 could have enhanced the spring effects of extreme variability in 2009, e.g. by

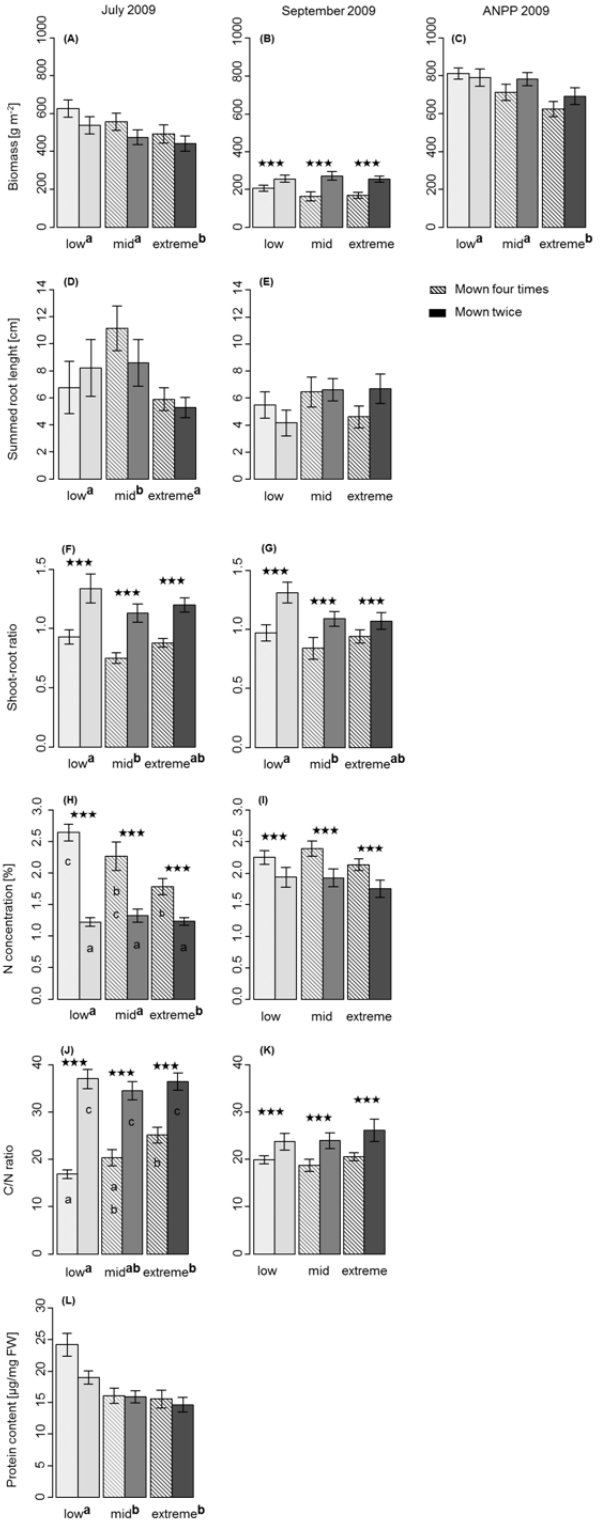

Figure 3 Plant response to altered rainfall variability with constant rainfall sum and to mowing frequency in 2009. Effects of low rainfall variability (light grey), intermediate rainfall variability (grey) and extreme rainfall variability (dark grey) and of mowing (patterned: four times; shaded: twice) on (A) early aboveground biomass in July, (B) late aboveground biomass in September, (C) aboveground net primary productivity, (D) summed root length in July, (E) summed root length in September, (F) early and (G) late shoot-root ratio, early (H) and late (I) N concentrations in leaves of *Alopecurus pratensis*, early (J) and late (K) C/N ratio in *Alopecurus pratensis* and (L) protein content in leaves of the legume *Trifolium pratense* on the last day of the drought treatment. Means ±1SE are shown, different superscript letters over the treatment names indicate significant differences below p=0.05 between the rainfall variability manipulations, asterisks indicate level of significance of differences between the two mowing frequencies (***<0.001) and different letters within the bar indicate differences in the post-hoc test between the subgroups, when the interaction between mowing frequency and rainfall variability was significant (only (H) and (J))

making soil more susceptible to drying. However, as the productivity trend is different from that observed at the end of 2008 (with no differences between the intermediate and low variability treatment in early 2009), we conclude that most of the effect can be attributed to altered spring rainfall variability.

4.2. Effects of increased rainfall variability with constant rainfall amounts

In 2009, which was naturally a wet year, the amount of rainfall that resulted from many small events (as in the low rainfall variability treatment) or from several moderate events (as in the intermediate rainfall variability treatment) did not discriminate soil moisture. The results show that very extreme rainfall events, as in the extreme variability treatment directly after drought, are not efficient in constantly increasing soil moisture, as they also increase water runoff and the length of the dry periods. Furthermore, long dry periods may reduce the water holding capacity of the soil or may even make the rhizosphere hydrophobic (Browning et al. 2007; Carminati et al. 2010), as indicated by the greater responsiveness of soil moisture toward dryness and the lower responsiveness to wet pulses in the extreme variability treatment. Our results provide evidence of a high short-term sensitivity of grassland after extreme spring rainfall variability that was neutralized until September. Nevertheless, ANPP was affected negatively by the extreme rainfall variability, indicating a possible risk of production losses for agriculture under global climate change. Comparable studies in mesic grassland also show losses in ANPP under increased rainfall variability: Heisler-White et al. (2009) report an 18% reduction in productivity, although the rainfall variability, which they applied, was greater (up to a 75% increase in the number of rainfall events) than in our experiment (a 33% reduction in events between extreme and low variability). Fay et al. (2003) and Knapp et al. (2002) report a 10% reduction in long-term productivity after subjecting mesic tallgrass prairie to more extreme rainfall patterns. Root length data in early summer indicate that extreme dryness, as well as regular water availability may decrease root biomass. Although enhanced root growth under drought is viewed as an adaptive feature of many species under drought, other studies also indicate that grassland roots may not respond with enhanced root growth to dryness (Kreyling et al. 2008a). Again, these changes to root length only became apparent in July and were thus relatively short-lived. However, the shoot–root ratio changed consistently as a result of changing rainfall patterns. The reduction of leaf N under extreme rainfall variability could be due to less microbial activity caused by low soil moisture and long dry periods, or even due to N leaching that is increased after extreme rainfall events (Heisler-White et al. 2008). Surprisingly, the protein content in the target legume *T. pratense* directly after drought was not affected by the extreme variability, but rather showed an increased protein content in the leaves under low rainfall variability, with no differences between intermediate and extreme rainfall variability. This indicates that the leaf quality of different functional groups reacts independently and differently toward rainfall variability. Furthermore, regular water availability might have increased the activity of N fixers in the nodules of *T. pratense.*

4.3. The effects of mowing frequency

The overcompensation in biomass production in more frequently mown communities in 2008 and early 2009 was reversed by a clear negative effect on productivity in September 2009. Most of the previous studies conducted on the effects of defoliation on productivity indicate either negative or neutral effects (Biondini et al. 1999; Green & Detling 2000; Hejcman et al. 2010; Leriche et al. 2003; Maron & Jeffries 2001; Milchunas & Lauenroth 1993), while the effects of overcompensation are reported mostly for very low or intermediate intensities of

cutting (Bernhardt- Römermann et al. 2011; Weigelt et al. 2009; Zhao et al. 2008) or for communities without any previous mowing history (Turner et al. 1993) and are often lessened after a history of several mowing events (Loeser et al. 2004). Our study also shows that overcompensation is reversed after one vegetation period of more frequent mowing. Our results therefore indicate that mowing history should be considered and adjusted to optimize productivity. Our findings of increased leaf quality in terms of N concentration and protein content are consistent with many other studies showing increased N concentration in leaves that were cut more frequently (Green & Detling 2000; Maron & Jeffries 2001; Turner et al. 1993). This might be explained by the generally lower shoot–root ratio in more frequently mown plots, caused by a reduced shoot biomass: this allows for a higher concentration of N in leaf tissue, as root biomass has to allocate resources to less aboveground biomass. Furthermore, increased defoliation intensity accelerates decomposition and N mineralization, thereby increasing the N level in the soil and thus mowing may enhance root N uptake and allocation to the shoots (Green & Detling 2000; Klumpp et al. 2009; Turner et al. 1993). Thus, although the effects of mowing on biomass production are ambivalent, the effects of mowing frequency on forage quality are unequivocally positive, as N, which is often a limiting factor for herbivores, increases.

4.4. Interactive effects between rainfall variability and mowing frequency

Mowing frequency and rainfall variability did not interact for most of the assessed parameters. Nevertheless, leaf N concentration and the C/N ratio in early summer were very responsive toward rainfall variability only in the more frequently mown plots, indicating a higher responsiveness of younger leaves with a lower shoot–root ratio toward extreme rainfall variability and drought. Grasses with a lower shoot–root ratio can allocate more N to the leaves; however, water availability is necessary for mineral uptake through the roots. As less frequently mown and thus older leaves have lower leaf N concentrations, they may not depend as largely on temporal water availability. In sum, although frequent mowing increases forage quality it might also increase the fluctuations in forage quality under climate change.

5. Conclusions

Our study shows that increased rainfall variability under climate change may cause losses in temperate grassland productivity and also reduces forage quality. In contrast to other studies, a comparison to the data of the previous year indicates that overall rainfall amount is more important for temperate grassland productivity than rainfall variability. However, changes in variability, that accompany changes in total rainfall amount, surely amplify the effects of differences in rainfall amount. Furthermore, our results indicate that mowing history might be more important for explaining productivity than mowing frequency alone. In sum, positive effects of more frequent mowing on forage quality might be diminished by increased rainfall variability just as increased rainfall variability alone negatively affects forage quality. To conclude, climate change will affect agriculture in Europe by changing meadow usability. Management strategies to buffer adverse effects on forage quality and quantity have yet to be investigated and established, as mowing frequency seems to have a rather small buffering capacity.

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Manuscript 4

Extreme weather events and plant-plant interactions – Shifts between competition and facilitation among grassland species in the face of drought and heavy rainfall

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Extreme weather events and plant-plant interactions – Shifts between competition and facilitation among grassland species in the face of drought and heavy rainfall

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Abstract

Biotic interactions play an important role in ecosystem function and structure in the face of global climate change. We tested how plant-plant interactions, namely competition and facilitation among grassland species, respond to extreme drought and heavy rainfall events. We also examined how the functional composition (grasses, forbs, legumes) of grassland communities influenced the competition intensity for grass species when facing extreme events. We exposed experimental grassland communities of different functional compositions to either an extreme single drought event or to a prolonged heavy rainfall event. Relative Neighbour Effect, Relative Crowding and Interaction Strength were calculated for five widespread European grassland species to quantify competition. Single climatic extremes caused species specific shifts in plant-plant interactions from facilitation to competition or vice versa but the nature of the shifts varied depending on the community composition. Facilitation by neighbouring plants was observed for *Arrhenatherum elatius* when subjected to drought. Contrarily, the facilitative effect of neighbours on *Lotus corniculatus* was transformed into competition. Heavy rainfall increased the competitive effect of neighbours on *Holcus lanatus* and *Lotus corniculatus* in communities composed of three functional groups. Competitive pressure on *Geranium pratense* and *Plantago lanceolata* was not affected by extreme weather events. Neither heavy rainfall nor extreme drought altered the overall productivity of the grassland communities. The complementary responses in competition intensity experienced by grassland species under drought suggest biotic interactions as one stabilizing mechanism for overall community performance. Understanding competitive dynamics under fluctuating resources is important for assessing plant community shifts and degree of stability of ecosystem functions.

Key-words:

Plant-plant interactions; Climate Change; community composition; competitive ability, facilitation; temperate grassland; drought; heavy rainfall

Introduction

Biotic interactions play a key role in the function and structure of ecosystems, influencing the provision of ecosystem services and patterns of biodiversity (Hillebrand et al. 2008; Cavieres & Badano 2009; Schweiger et al. 2010). Biotic interactions, such as competition and facilitation among plants, affect the abundance and distribution of species (Davis et al. 1998).

All species within a plant community compete for the same resources, such as water, light, nutrients or space. Minor differences among species in environmental requirements promote species coexistence via niche differentiation (Whittaker 1965; Tilman 1982). Additionally, species can facilitate the invasion, coexistence, establishment or growth of other species by amelioration of their environment (Brooker et al. 2008; Armas et al. 2008; Schöb et al. 2013; Gross et al. 2013). For example, legumes can promote neighbouring plants due to their ability to fix additional atmospheric nitrogen which increases the nitrogen content in the soil (Arfin Khan et al. 2014). Further, plants of different growth forms can alter the canopy structure of plant communities (Tremmel & Bazzaz 1993) resulting in competitive hierarchies with effects on the plant performance due to the directional supply of light (Keddy & Shipley 1989; Anten & Hirose 1999; Hautier et al. 2009). Thus, plant communities exhibit a particular suite of dominant and minor species as a result of particular combinations of biotic interactions (Walker et al. 1999; Brooker 2006).

Due to climate change, extreme weather events, such as drought and heavy rainfall, are increasing in frequency and magnitude (IPCC 2012). Biotic interactions, such as competition and facilitation, are expected to mediate the effects of climate change, yet they are still not well understood (Jiang & Kulczycki 2004; Hulme 2005; Brooker 2006; Adler et al. 2006; Lavergne et al. 2010; Hillyer & Silman 2010). Thus, only few hypotheses exist on how extreme weather events will alter plant-plant interactions (Brooker 2006; Miranda et al. 2009; Levine et al. 2010; Soliveres et al. 2013). According to the 'stress- gradient hypothesis' introduced by Bertness and Callaway (1994), facilitation should be more common when plants are subject to high abiotic stress. This is supported by observations from environments with severe climatic or edaphic conditions which suggest that neighbouring plants are more facilitative and might increase community resistance under stressful conditions (Holmgren et al. 1997; Bertness & Ewanchuk 2002; Maestre et al. 2003; Brooker et al. 2008; He et al. 2013). In contrast, some studies have found that competition may increase with elevated stress regimes (Chen et al. 2009; Saccone et al. 2009). Under extremely severe environmental conditions, biotic interactions may become unimportant, relative to the effect of the abiotic stress, thus only the most stress-tolerant species can persist (Michalet et al. 2006; Maestre et al. 2009; Saccone et al. 2009). The balance between competition and facilitation can be further influenced by factors such as plant density and physiology, life stage, and invasion of species (Callaway & Walker 1997; Manea & Leishman 2011), which might also be altered by climate change.

Evidence suggests that facilitation is more likely and stronger under drought than under moist conditions (Callaway & Walker 1997; Holmgren et al. 1997; Kikvidze et al. 2006; Sthultz et al. 2007; Tylianakis et al. 2008). The majority of these studies stem from semi-arid or arid habitats, therefore it is unclear if drought events will also increase facilitative interactions in temperate grassland. Moreover, very little is known regarding the effects of heavy rainfall events on plant-plant interactions. Hypoxia in the rhizosphere, as a consequence of waterlogged soils after heavy rainfall events, could impair plant performance due to reduced photosynthetic activity and growth, or due to nutrient deficiency and toxicity (Steffens et al. 2005; Irving et al. 2007). Previous work simulating extreme rainfall has shown that the competitive balance of most species was unaffected by rainfall treatment, and only some grasses showed reduced competition intensity under heavy rainfall (White et al. 2001).

Understanding the role of plant-plant interactions under extreme weather events is important for modelling and projecting plant community dynamics and the stability of ecosystem functions under climate change. Therefore, we examined the effects of extreme weather events on plant-plant interactions by simulating extreme drought and heavy rainfall events. We investigated the response of five grassland species grown in three experimental communities differing in functional composition and quantified changes in the biotic interactions among these plants.

We hypothesize that

(i) extreme drought will decrease competition intensity among grassland species due to facilitation by neighbouring plants and that

(ii) extreme heavy rainfall will only reduce the competition intensity experienced by stress-tolerant species due to lower competition with their struggling neighbours.

(iii) Further, we expect that the presence of forbs or legumes in the grassland community will alter the biotic interactions of grass species under extreme weather events.

Materials and methods

Experimental design

Our study is part of the EVENT I experiment analysing the effects of extreme weather events and plant diversity on ecosystem functions (Jentsch et al. 2007). The experimental site is located in the Ecological Botanical Garden of the University of Bayreuth, Germany (49°55'19''N, 11°34'55''E, 365 m a. s. l.). The mean annual temperature for Bayreuth is 8.2°C, and the mean annual precipitation is 724 mm (data: German Weather Service, 1971 – 2000). The experiment was carried out in a split-plot design, manipulating (i) precipitation (drought and heavy rainfall events) and (ii) plant community composition. The three plant communities were blocked and randomly assigned within the two weather manipulations and control, with every combination having five replicates. Thus, the setup consisted of a total of 45 plots with a size of 2x2 m. In addition, one plant individual of each species was grown in isolation within each replicated treatment block using buried tubes (∅ 20 cm, h = 30 cm) next to the plots. The isolated plants (n=5 per species and treatment) were exposed to the same weather manipulations. The species composition and plant isolation installed in 2005 has been maintained by periodic weeding. Before this study in 2007, the plant communities were already pre-exposed to manipulated extreme drought and rainfall events in 2005 and 2006, though community biomass had not changed in the weather treatments during these years (Kreyling et al. 2008; Mirzaei et al. 2008). Biomass of plant individuals which grew in isolation was also unaffected by weather treatments, except for *Lotus corniculatus* which decreased due to drought compared to control in 2005.

The texture of the previously homogenized soil consists of loamy sand (82% sand, 13% silt, 5% clay) with pH = 4.5 in the upper (0 cm - 20 cm), and pH = 6.2 in the lower, soil layer (measured in 1 M KCl). Drainage pipes at approximately 80 cm soil depth minimized lateral water flow. Data acquisition was only carried out in the central square meter of each plot in order to avoid edge effects.

The weather manipulations consisted of extreme drought and heavy rainfall. Ambient weather conditions were used in the control plots. Intensity of the treatments was based on

the local 100-year extreme event in each category. Data from growing seasons (March to September) from 1961–2000 were used as the reference period (data: German Weather Service). The Gumbel I distribution (Gumbel 1958) was fitted to the annual extremes, and 100-year recurrence events were calculated. Drought was defined as the number of consecutive days with less than 1 mm of daily precipitation. Accordingly, a drought period of 32 days (May 21-June 21, 0 mm d^{-1}) and a rainfall extreme of 170 mm over 14 days (June 8-

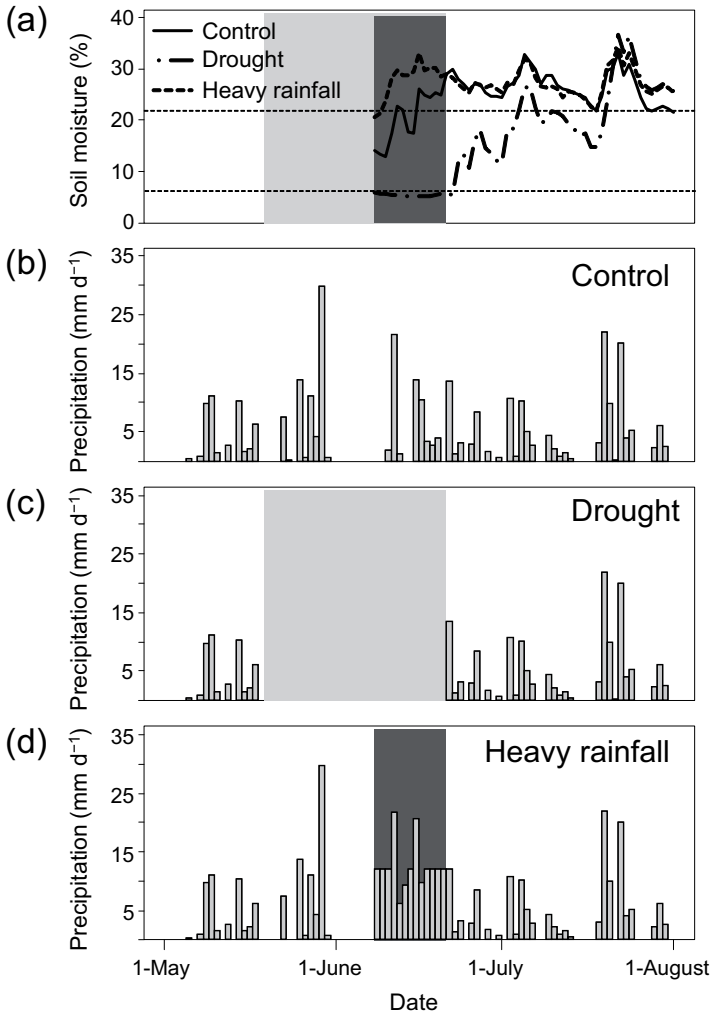

Figure 1 Mean daily soil moisture (a) and daily sum of precipitation in the EVENT experiment during manipulation of drought (c) and heavy rain events (d) and following recovery. Soil moisture (vol.%) at 5 – 10 cm depth was recorded in all grassland plots with two functional groups using FD sensors (Echo.EC-5/k, Decagon). Dashed lines indicate permanent wilting point (6 vol.%) and field capacity (22 vol.%).Timing and duration of the weather manipulations are indicated by grey shaded areas (drought: light grey, heavy rainfall: dark grey). Soil moisture in weather manipulation is significant different form ambient conditions (b) within manipulation period (Linear mixed effect model $F = 478$ $p < 0.001$). Due to technical problems no soil moisture data was available before June 7th.

Extreme weather events

June 21, 12.1 mm d^{-1}) were applied in the experiment during the peak growing season in 2007 (Fig. 1). Drought was simulated using rain-out shelters, constructed with steel frames (Hochtunnel, E & R Stolte GmbH, Germany) and covered with transparent plastic sheets

(material: 0.2 mm polyethylene, SPR 5, Hermann Meyer KG, Germany) that permitted nearly 90% penetration of photosynthetically active radiation according to tests prior to set-up. Strong greenhouse effects were avoided by placing the roof 80 cm above ground level, allowing for near-surface air exchange. Heavy rainfall was simulated using portable irrigation systems. Drop size and rainfall intensity resembled natural heavy rainfall events through application by Veejet 80100 nozzles. The total amount of added water was divided into two applications per day to ensure constantly high soil water content. If natural precipitation occurred, the amount of rain was deducted from the respective dose. Lateral surface flow was avoided through the application of small plastic sheet pilings around treated plots.

Experimental plant communities

Five wide-spread plant species of the regional flora were chosen. Species were selected with respect to their life-span (perennials), their overall importance in nearby and Central European grassland systems, and based on whether they naturally grow on substrate similar to that used in this experiment (Table 1). We have chosen grasses and forbs as the most dominant functional groups of grasslands (Bazzaz & Parrish 1982). Additionally, we added a legume species due to its ability to fix atmospheric nitrogen, which is seen to be facilitative for grasses under ambient conditions (Quinos et al. 1998). Plant individuals in defined quantitative composition were planted in a systematic hexagonal grid with 20 cm distance between individuals in early April 2005. Grassland plots were established in three combinations with an increasing number of plant functional types (Table 1). The experimental communities represent naturally occurring species combinations despite being reduced to two or four species for inevitable experimental simplification. Repetitions with other species combinations of the tested functional groups or monocultures of the grasses were not considered. The results, especially concerning the legume, could be caused by sampling effects of *Lotus corniculatus* as well as a legume effect.

Table 1 Composition of the experimental grassland communities with three functional group combinations

Species combinations	Functional group number	Functional group types
Arrhenatherum elatius, Holcus lanatus	1	2 grasses
Arrhenatherum elatius, Holcus lanatus, Plantago lanceolata , Geranium pratense	2	2 grasses, 2 forbs
Arrhenatherum elatius, Holcus lanatus, Plantago lanceolata, Lotus corniculatus	3	2 grasses, 1 forb, 1 legume

Response parameter: biomass of plant individuals and community biomass

Our interest was the direct effect of the extreme weather events on the competitive balance among the grassland species. Thus, plant data were collected 10 days after the end of drought and heavy rainfall manipulations. At this date, we expected the largest manipulation effect on our response parameter for plant performance (aboveground biomass) on which the calculation of the competition indices is based. Aboveground biomass was quantified for all five grassland species by harvesting four individuals per plot separately (pseudo replicates) out of the central square meter on July 2nd. After harvesting the individuals, the remaining material of all plants in the inner square meter of each plot was harvested and

sorted by species, which added to the harvested individuals forms the community biomass. Furthermore, plant individuals of each species, which were grown in isolation next to the plots, were harvested separately. All harvested biomass was dried at 75°C to constant weight and weighed.

Calculation of competition indices

In this study, mathematical indices were used to quantify plant competition. This is a common and widespread method (Weigelt & Jolliffe 2003) but is also a topic of debate. The methodological challenges for tracking shifts in competitive balance with rapid changes in resources, and the usefulness of competition indices to quantify competition under changed environments is controversial (Freckleton and Watkinson 1997a, 1997b; Markham 1997; Freckleton and Watkinson 1999; Peltzer 1999). Competition indices cannot distinguish between inter- and intraspecific competition when environmental conditions change, because they neglect the yield-density relationship (Freckleton & Watkinson 1997b). We used the Relative Neighbour Effect (RNE) introduced by Markham and Chanway (1996) in order to quantify shifts in competitive intensity. We interpret the general competitive variation under extreme weather events knowing that also individuals of the same species will probably contribute to this interaction. Thus, RNE, the effect of neighbours relative to the plant with the greatest performance, was calculated according to equation 1.

$$RNE = \frac{(y_{iso} - y_{mix})}{x} \qquad \text{eqn 1}$$

with $x = y_{iso}$ if $y_{iso} > y_{mix}$ and $x = y_{mix}$ if $y_{mix} > y_{iso}$

Where RNE (unitless) is Relative Neighbour Effect ($-1 \leq RNE \leq +1$), y_{iso} is the performance per plant, in this case biomass, for a plant individual growing alone and y_{mix} is the biomass per plant for a plant individual growing in a mixed community. Negative and positive values indicate respectively facilitation and competition by neighbours (Markham & Chanway 1996).

Furthermore, to track whether altered plant-plant interactions were due to crowding caused by altered environmental conditions or due to changed competition abilities of single species, the Relative Crowding (D_r') and the Interaction Strength (I) were calculated following the approach of Wilson (2007).

Relative Crowding (D_r') measures the relative degree of crowding by competitive neighbours whose growth might be altered by changes in habitat conditions, proportionally to the abundance of the neighbours present (Wilson 2007). It can be seen as a measure for competition related to the density or size of neighbour plants. High D_r' values indicate highly productive neighbours and therefore high crowding pressure on the target plant. D_r' is calculated as followed

$$D_r^{'} = \frac{z_{mix}}{\max(y_{iso}, y_{mix})} \qquad \text{eqn 2}$$

where $D_r^{'}$ (unitless) is the generalized effect of Relative Crowding ($Dr' \geq 0$), z_{mix} is abundance of neighbour plants surrounding the target plant (g m^{-2}), y_{iso} is the biomass of a target plant growing in isolation and y_{mix} is the biomass of a target plant growing in a mixture. The abundance of neighbours surrounding the target plant (z_{mix}) was determined using the total plot biomass minus the weight of the target plant.

If there are plants which do not compete for shared limiting resources, the performance of a target plant will decrease less than a plant surrounded by neighbours with active or similar resource demands (Wilson 2007). In addition, suppression will occur throughout the range of

actual neighbour abundance. Therefore, the Interaction Strength I (unitless), a measure for the suppression of the target plant performance per neighbour biomass, is calculated as followed

$$I = \frac{y_{iso} - y_{mix}}{z_{mix}} \qquad \text{eqn 3}$$

Low I values show low suppression of the target plant performance by neighbouring plants and indicates the high competitive ability of the target plant in gaining the shared limiting resources.

Statistical analyses

We performed linear mixed effect models in combination with an ANOVA to test for significant effects of weather manipulation and community compositions, and their respective interactive effects on the response variables. The response variables were biomass, RNE, I and D_r'. We took the split plot design and pseudo replicates into consideration by adding 'repetition', 'plot' and 'individual number' as random factors. The model was simplified if no significant interaction was found by using weather manipulation or community composition as fixed factors. In order to validate the linear mixed effects models, residuals versus fitted plots and plots showing sample quantiles versus theoretical quantiles based on the model were checked for homogenous variance and normal distribution of residuals (Faraway 2006). If conditions of normality were not met or if data required an improved homogeneity of variance, data of biomass and Relative Crowding were transformed using log(y+1). In all tests the level of significance was set to p = 0.05. All statistical analyses were performed using the statistical software R 2.4.1 (R Development Core Team 2006). For linear mixed effect models the software package "lme4" (Bates & Sarkar 2007) was used. Additionally, the package "multcomp" (Hothorn et al. 2007) was applied for multiple post-hoc comparisons. The results of the post-hoc comparison for specific treatment pairs are indicated by p-values without information on F-values and degrees of freedom.

Results

Drought effects on RNE on grassland species

We found mixed responses of Relative Neighbour Effect (RNE) to extreme drought, which varied across species. *Arrhenatherum elatius* was significantly facilitated by neighbouring plants under drought compared to controls in the communities where it was growing with one more grass species (Fig. 2a, p = 0.006) or with two grass and two forb species (Fig. 2a, p = 0.049). However, *Lotus corniculatus* RNE increased significantly under extreme drought compared to controls, (Fig. 2e, p = 0.041) representing a shift from facilitation to competition by neighbours. *Geranium pratense* and *Plantago lanceolata* had positive RNE values (Fig. 2c,d) both under ambient conditions and when exposed to extreme drought. However, RNE on *G. pratense* was marginally lower in the drought treatment than under ambient conditions (p = 0.093), indicating competitive release. Competition intensity experienced by *Holcus lanatus* was not affected by drought (Fig. 2b).

Heavy rainfall effects on RNE on grassland species

Heavy rainfall caused alterations of plant neighbour effects on two of the five studied grassland species. RNE on *L. corniculatus* and *H. lanatus* increased significantly under heavy rainfall compared to controls (Fig. 2, $p = 0.002$ and $p = 0.012$) representing a shift from facilitation to competition by neighbours. However, the higher competitive pressure of neighbouring species on *H. lanatus* individuals after heavy rainfall was found only in communities composed of three functional groups. Heavy rainfall did not alter the neighbour effects on *A. elatius, P. lanceolata* and *G. pratense* compared to ambient weather conditions (Fig. 2a,c,d). However, in communities composed of two functional groups, the competitive pressure on *G. pratense* was significantly higher than on all other species when subjected to heavy rainfall (interaction weather treatment x species: $F_6 = 2.47$ $p = 0.025$). Furthermore, RNE on *A. elatius* was significantly higher compared to RNE on *L. corniculatus* under ambient weather conditions in communities composed of three functional groups. This difference disappeared in the heavy rainfall treatment. None of the five species were significantly facilitated by neighbouring plants under heavy rainfall compared to ambient weather conditions.

Grass species interactions in communities with altered functional composition

The grass species *A. elatius* and *H. lanatus* increased in the degree of crowding with increasing number of functional groups (Fig. 3, $F_2 = 34.6$ $p < 0.001$ and $F_2 = 72.8$ $p < 0.001$). The Relative Crowding on *A. elatius* was significantly higher in the heavy rainfall treatment (Fig. 3a) compared to control and drought treatment. Relative Crowding on *H. lanatus* was not affected by weather treatments (Fig. 3b, $F_2 = 0.6$, $p = 0.561$). Under extreme drought, Interaction Strength of *A. elatius* was significantly decreased compared to controls with the exception of communities with three functional groups (Fig. 4a). The Interaction Strength of *H. lanatus* per unit neighbour mass increased with heavy rainfall in presence of three functional groups (Fig. 4b, $p = 0.047$). In general, the competitive effect of neighbouring plants on *A. elatius* rose with increasing number of functional groups ($F_2 = 5.3$, $p = 0.006$). However, RNE on *H. lanatus* changed with altered community composition (Fig.2b, $F_2 = 3.3$ $p = 0.040$) without clear direction.

Aboveground biomass of species individuals and grassland communities

Aboveground biomass of isolated individuals of *A. elatius* decreased by drought ($p = 0.019$, Fig. 5a) and heavy rainfall ($p < 0.001$) compared to controls, whereas biomass of isolated *L. corniculatus* individuals increased by drought and heavy rainfall (both treatments $p < 0.001$; Fig. 5e). Biomass of individuals grown in mixtures responded only to extreme heavy rainfall (Fig. 5). Biomass of *L. corniculatus* grown in communities composed of three functional groups was lower in the heavy rainfall treatment than under ambient conditions ($p = 0.013$). *H. lanatus* and *A. elatius* showed reduced individual biomass only in communities composed of three functional groups ($p = 0.002$ and $p = 0.049$), though biomass of both species individuals in communities with two grass species was marginally lower in heavy rainfall compared to controls ($p = 0.092$ and $p = 0.058$). Total community biomass was not affected by extreme drought or heavy rainfall compared to ambient weather conditions ($F_2 = 0.4$, $p = 0.668$). Communities with most functional groups including the legume species *L. corniculatus* were always the most productive ($F_2 = 103.6$, $p < 0.001$).

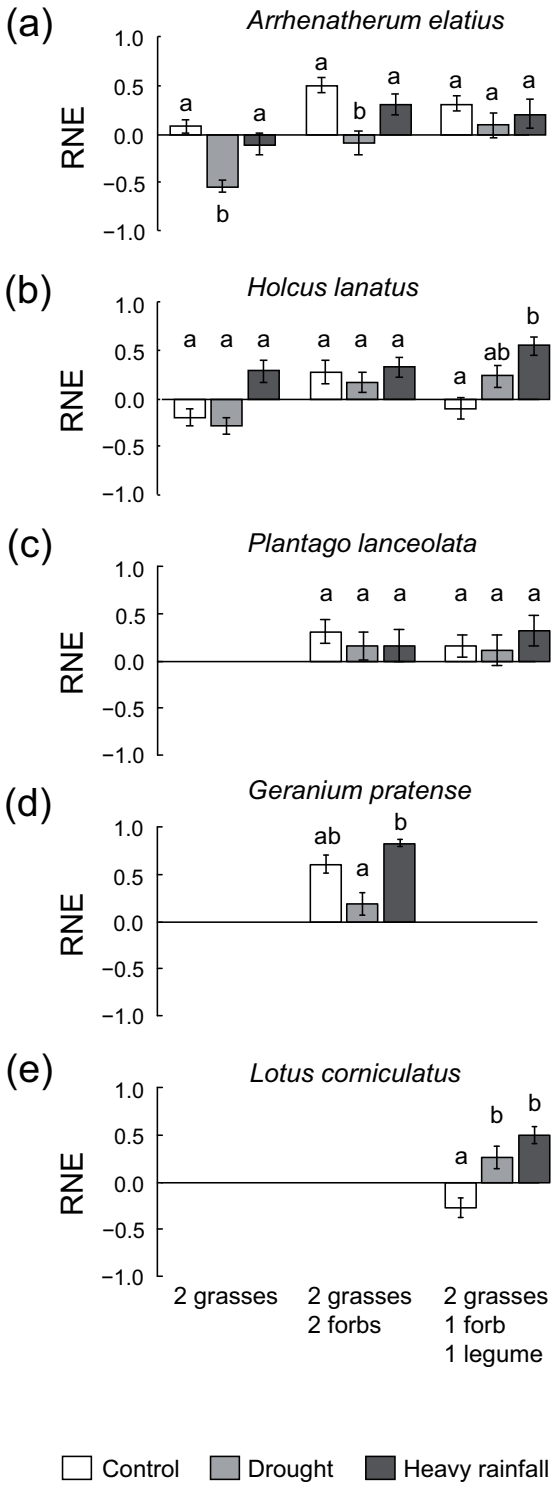

Figure 2 Relative Neighbour Effect (RNE) on (a) *Arrhenatherum elatius,* (b) *Holcus lanatus,* (c) *Plantago lanceolata*, (d) *Geranium pratense*, and (e) *Lotus corniculatus* in three different community compositions under the weather treatments drought, heavy rainfall and control. Mean value and one standard error for each species in each community are given. Small letters indicate significant differences between weather treatments for a given community ($p < 0.05$).

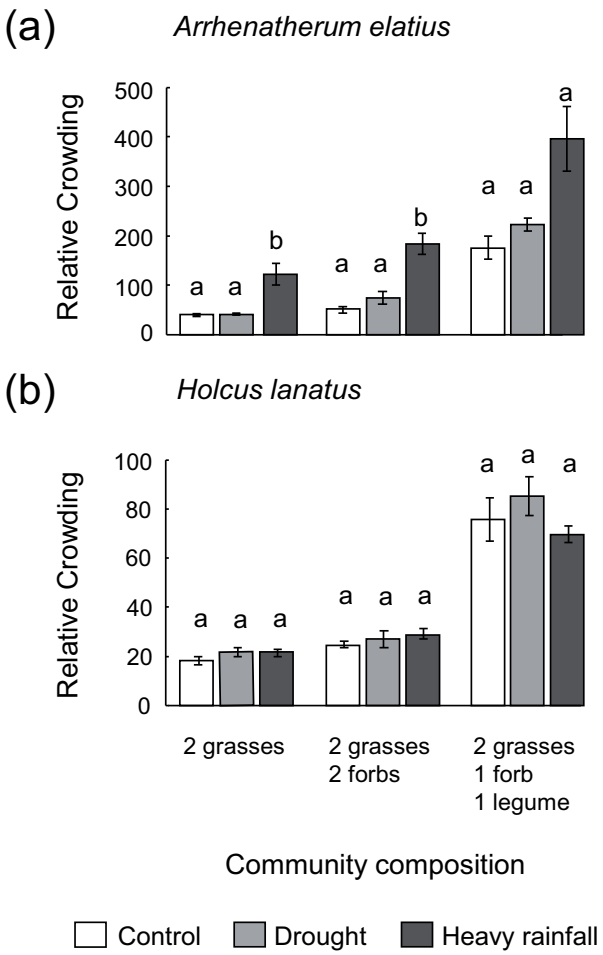

Figure 3 Relative Crowding on (a) *Arrhenatherum elatius* and (b*) Holcus lanatus* in three different community compositions under the weather treatments drought, heavy rainfall and control. Mean value and one standard error for each species in each community are given. Small letters indicate significant differences between weather treatments for a given community ($p < 0.05$).

Discussion

Plant-plant interactions in response to drought

We found indications of facilitation by neighbouring plants in the face of drought. *A. elatius* was facilitated by its neighbours when it grew in communities with the grass species *H. lanatus* and in communities with *H. lanatus, G. pratense and P. lanceolata.* Furthermore, *G. pratense* tended to be subjected to a lower competitive effect from neighbouring plants when exposed to drought. This could be indicative for release from competition with respect to growth under ambient conditions. Similar responses have been found in other field experiments, where facilitative effects were more evident in dry and hot years (Callaway & Walker 1997), and where positive effects became stronger as abiotic stress increased (Callaway 1997). There may be a nursing effect caused by neighbouring plants which cast shade and therefore lead to lower transpiration demands, increased soil water availability and improved conditions for root growth (Holmgren et al. 1997; Armas et al. 2008; Schöb et al. 2013). In addition, the anatomy of the neighbouring species *H. lanatus* and *G. pratense* regarding water and gas exchange is mesomorphic to hygromorphic (Ellenberg 1979) and we can assume that they might not be as effective as *A. elatius* in the use of the “additional” resources. *A. elatius* is expected to better exploit water from soils than other grasses due to its extensive root systems (Grime et al. 2007).

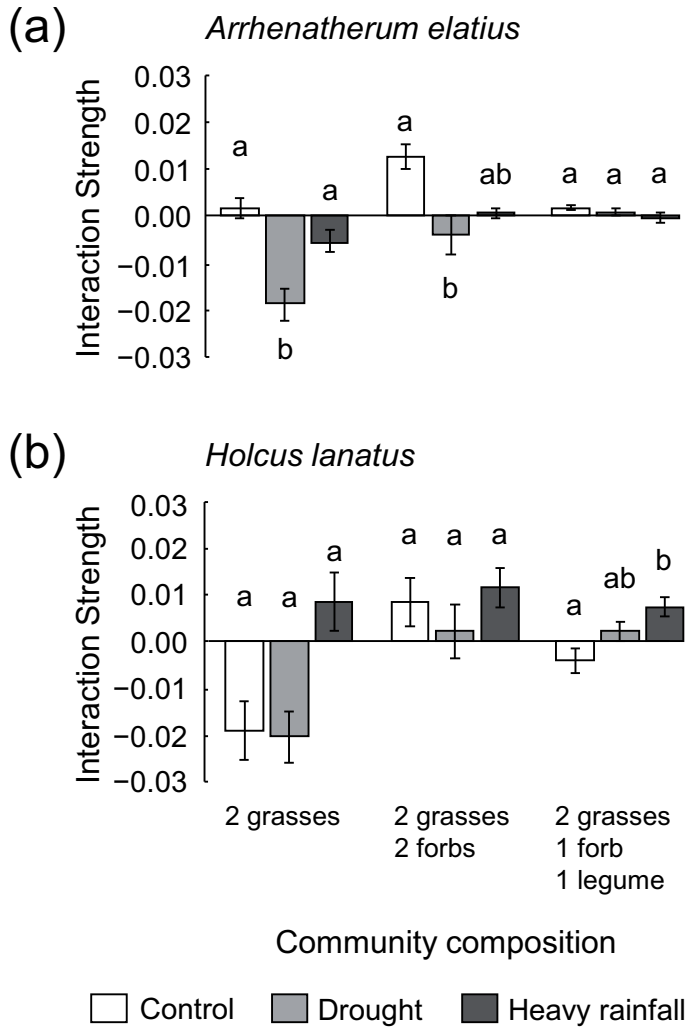

Figure 4 Interaction Strength of (a) *Arrhenatherum elatius* and (b) *Holcus lanatus* in three different community compositions under the weather treatments drought, heavy rainfall and control. Mean value and one standard error for each species in each community are given. Small letters indicate significant differences between weather treatments for a given community ($p < 0.05$).

The neighbourhood of the legume species *L. corniculatus* shifted from facilitative to competitive conditions under drought. Under ambient weather conditions, *L. corniculatus* had a competitive advantage most likely due to its ability to fix additional atmospheric nitrogen which led to bigger plant individuals compared to other species in this study. Drought very likely disrupted this competitive advantage. Abdelhamid et al. (2011) showed that the drying of the upper soil layer affected the root nodules and reduced the proportion of nitrogen derived from the atmosphere of *Vicia faba*. Furthermore, Arfin Khan et al. (2014) found that the presence of a legume species facilitated the community productivity of non-legume neighbour plants under ambient weather conditions but not under recurrent drought events. However, they saw reduced N-uptake rather than reduced N-fixation by the legume as an explanation for the missing facilitative legume effect under drought. Water is the major solvent and transport agent for nutrients and therefore it controls the nitrogen cycle (Akmal & Janssens 2004). The combination of water and nitrogen deficits limits plant productivity (Sadras 2005).

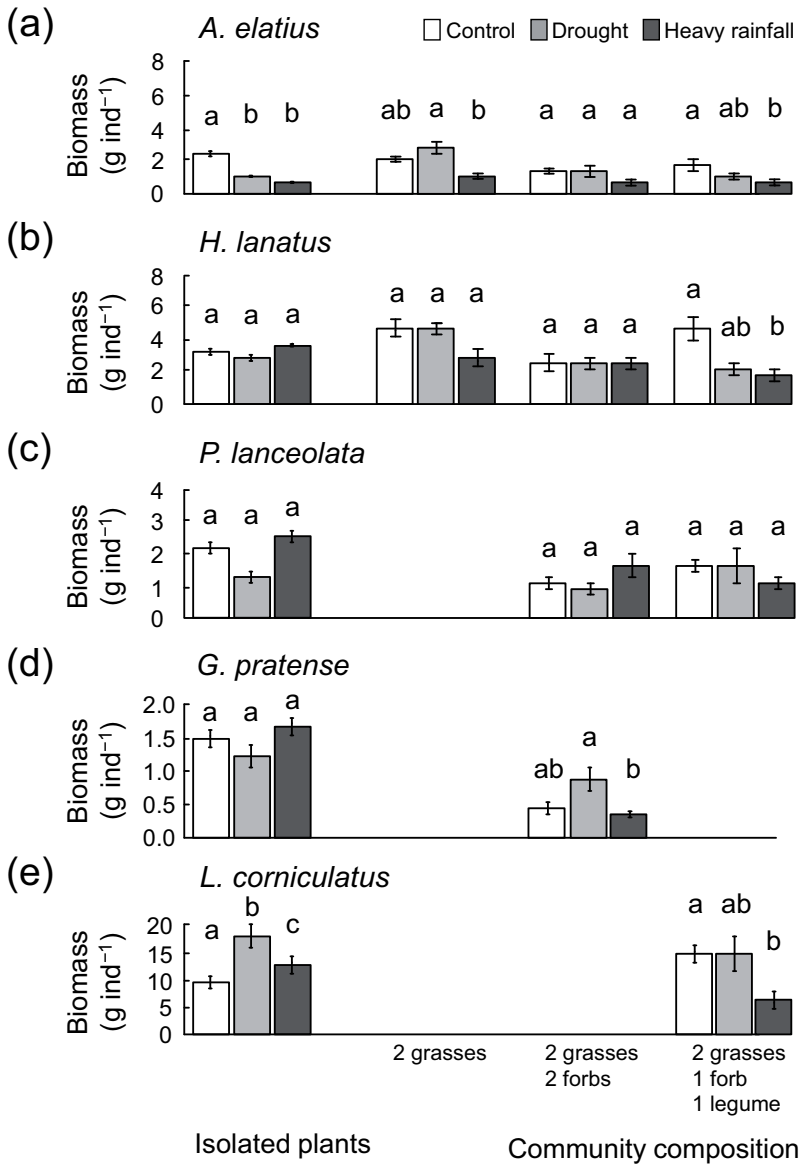

Figure 5 Aboveground biomass of plant individuals of (a) *Arrhenatherum elatius,* (b) *Holcus lanatus,* (c) *Plantago lanceolata*, (d) *Geranium pratense*, and (e) *Lotus corniculatus* grown in isolation or in three different communities compositions under the weather treatments drought, heavy rainfall and control. Mean value and one standard error for each species in each community are given. Small letters indicate significant differences between weather treatments for a given community ($p < 0.05$).

Hence, we can only confirm our first hypothesis – that under extreme drought competitive intensity will decrease – for one out of five studied species, as we also found inverse reactions within one of our study species. However, the facilitation of the competitor *A. elatius* in two plant communities and the increased competitive effect on the stress-tolerant-CSR-strategist *L. corniculatus* (Grime et al. 2007) support the idea that competitors are more facilitated than the stress-tolerators (Michalet et al. 2006).

Plant-plant interactions in response to heavy rainfall

Neighbouring plants imposed significantly more competitive pressure upon *L. corniculatus* and *H. lanatus* in communities composed of three functional groups when facing a heavy rainfall event. This contrasts with the findings of White et al. (2001) who found no effects on competitive intensity for grasses under extreme rainfall. However, several studies from arid or semi-arid systems observed competition rather than facilitation under a 'less dry situation' (Holmgren et al. 1997). The higher competition experienced by *L. corniculatus* and *H. lanatus* suggest that this tendency toward competition exists also under very wet conditions – such as water-logging due to heavy rainfall – and also applies for a mesic grassland system. Furthermore, with increased soil moisture other factors, such as light, might become more important and limiting (Holmgren et al. 1997, 2012; Novoplansky & Goldberg 2001). Thus, the canopy of neighbouring plants and its shading function might have increased the constraint for the target plants. This is indicated by highest Relative Crowding in the community including legumes and by the reduced biomass of *L. corniculatus* grown in mixture, compared to the increased biomass of isolated individuals due to heavy rainfall. Furthermore, the decrease in individual biomass of three of the target species in the mixture and in isolated biomass of *A. elatius* plants in response to heavy rainfall indicates that photosynthesis and transpiration were reduced as a consequence of decreased soil oxygen due to water-logging (compare Striker et al. 2005).

Reduced soil oxygen due to water-logging during the heavy rainfall event may limit the symbiosis between the legume *L. corniculatus* and nitrogen-fixing bacteria as a result of reduced oxygen transport in submerged nodules (James & Crawford 1998). This phenomenon may explain the reduced competitive advantage of *L. corniculatus* observed and the increased competitive effects of neighbouring plants on *L. corniculatus*.

The results for *H. lanatus* and *L. corniculatus* imply higher competition as opposed to facilitation for plants subjected to heavy rainfall. Facilitation by neighbouring plants for these grassland species was not visible when subjected to heavy rainfall. Thus, we have to reject our second hypothesis because we did not find species that were facilitated by the suppression of other species which struggle under heavy rainfall.

Grass species interactions in communities with altered functional composition

The importance of community composition for plant-plant interactions was indicated by alterations in competitive pressure of neighbouring plants on our target species *A. elatius* and *H. lanatus*. It is not surprising that with increasing number of species and functional groups the competition by density and size of neighbours (Relative Crowding) and the general competitive pressure (RNE) increased. Zhang et al. (2008) mentioned that species response to the stress imposed by changed environments can be modified or amplified by the presence of coexisting species. The facilitative effect of neighbouring plants on *A. elatius* was found in two of the three communities. Given that Relative Crowding was not affected by drought, this reduced competitive effect was mostly caused by higher competitive ability and a lower decrease in performance of *A. elatius* in the communities composed of one or two functional groups, as indicated by the decreased Interaction Strength. With the addition of another functional group – the legume *L. corniculatus* – into the community, neighbour effects on *A. elatius* were competitive in all treatments, caused by lower competitive ability of *A. elatius* (I) and the higher competition by neighbour abundance (D_r').

The increase of competition induced by heavy rainfall experienced by *H. lanatus* was most pronounced in the presence of *L. corniculatus,* since the competitive ability of *H. lanatus* to gain the shared limiting resources decreased. There are controversial studies on the benefit for grasses grown in mixture with legumes (Quinos et al. 1998; Zhang et al. 2008). Ledgard and Steele (1992) noted that factors favouring legume performance decreased the performance of associated grasses and also that stress on legumes enhanced the competitiveness of grasses. The shift from facilitation to competition for *L. corniculatus* under drought and heavy rain and the modified responses of the tested grasses in the communities which included the legume indicate that a legume might play a key role in plant-plant interactions under climate change. However, we did not repeat our test with community compositions of other species, so that our findings might be a sampling effect of *L. corniculatus*. Further experiments are required with other species combinations to confirm the generality of our results. Nevertheless, these results provide evidence of climate extremes and induced alterations in competitive intensity including facilitation and competition among species, depending on the complexity of community composition.

Shifting directions of plant-plant interactions – one important mechanism for stability in aboveground biomass?

We found that aboveground biomass of the grassland communities was not altered by extreme drought or heavy rainfall events, although soil moisture was significantly reduced and increased, respectively, implying high plant water stress. Plant water stress was demonstrated during the same drought event in the same plots and year (Otieno et al. 2012), this was expressed as a decline of leaf water potential and less negative delta ^{13}C for *A. elatius*. Other studies have confirmed that plant communities facing extreme weather events are more stable than previously thought (Jentsch et al. 2011; Miranda et al. 2011; Lloret et al. 2012). There are several possible factors influencing the stability of plant community functioning in multi-species communities, such as complementary resource use, resilience of dominant or keystone species, or redundancy of species roles (Hooper et al. 2005). Species rich communities are hypothesized to insure ecosystem performance because they likely contain plant species which can compensate if other species suffer or die due to fluctuating environments (Yachi & Loreau 1999). Accordingly, plant species that are of minor importance today can become more relevant if previously dominant or more competitive species decline or fail in the face of climate change (Walker et al. 1999).

Neighbour effects can easily shift from competition to facilitation and vice versa, because what is facilitative for one plant might be negative for another plant (Holmgren et al. 1997). Thus, shifts in competitive intensity among species may prove to be a key mechanism contributing to the stability of plant community productivity under extreme weather events. In this study, the grassland species showed species specific responses in competition intensity to the extreme events. This species specific response is in accordance with other studies and can result from species specific optima and stress-tolerance as well as from possible modifications or amplifications induced by other species (Zhang et al. 2008). However, especially for drought, the event led to opposite species interactions. Facilitation strongly countered the direct effect of drought on *A. elatius* as isolated individuals were smaller than individuals grown in mixtures and probably helped to stabilize the biomass of the communities without the legume. Greater competition under drought prevented *L. corniculatus* from increasing the community biomass, although drought led to increases of this species when grown in isolation.

Conclusion

Our snapshot on the plant-plant interactions at the peak of abiotic plant stress due to extreme drought and heavy rainfall events in artificial grassland communities indicates that the competitive behaviour of grassland species can be species specific and reciprocal under the influence of extreme weather events. Single climatic extremes caused shifts in plant-plant interactions from facilitation to competition or vice versa for *A. elatius, H. lanatus* and *L. corniculatus*, but the nature of the shifts varied depending on the community composition. The presence of a legume in the plant communities appeared to have a key role in the response of competition intensity experienced by grasses to climate change. Furthermore, our results for plant-plant interactions suggest that a change in competitive balance among grassland plants might be one of the mechanisms for stable community productivity in the face of drought. Therefore, contrasting biotic interactions between grassland species should be acknowledged when modelling plant-plant interactions and predicting plant community shifts due to climate change.

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Manuscript 5

Climatic extremes lead to species-specific legume facilitation in an experimental temperate grassland

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Climatic extremes lead to species-specific legume facilitation in an experimental temperate grassland

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Abstract

Background Nitrogen-fixing legumes are key species in grassland ecosystems, as their ability to fix atmospheric nitrogen can facilitate neighboring plants. However, little is known about the fate of this legume effect in the face of extreme weather events, which are increasingly expected to occur.
Methods Here, we examined experimentally how the presence of a legume modifies above-ground net primary production (ANPP) and nitrogen supply of neighboring non-legumes under annually recurrent pulsed drought and heavy rainfall events by comparing responses of three key species in European grassland versus without legume presence over 4 years.
Results Legume presence facilitated community productivity of neighboring non-legumes under ambient weather conditions and also under experimental heavy rainfall. However, no facilitation of community productivity by the legume was found under experimental drought. Productivity of the three target species responded species-specifically to legume presence under different weather conditions: *Holcus lanatus* was facilitated only under control conditions, *Plantago lanceolata* was facilitated only under heavy rainfall, and *Arrhenatherum elatius* was facilitated irrespective of climate manipulations. The legume effects on $\delta^{15}N$, leaf N concentration, and N uptake were also species specific, yet irrespective of the climate manipulations. The data suggest that the missing legume effect on community productivity under the pulsed drought was rather caused by reduced N-uptake of the target species than by reduced N-fixation by the legume.
Conclusions In contrast to heavy rain, the presence of a legume could not effectively buffer community ANPP against the negative effects of extreme drought events in an experimental temperate grassland. Facilitation also depends on the key species that are dominating a grassland community.

Introduction

The presence of nitrogen fixing legumes has positive effects on productivity in Central European grassland ecosystems (Temperton et al. 2007; Marquard et al. 2009; Küchenmeister et al. 2012; Roscher et al. 2012). Evidence suggests that the effects of declining species richness on ecosystem functioning can partly be buffered by the presence of key species that control the functioning of communities (Beierkuhnlein & Jentsch 2005; Hooper et al. 2005). Legumes are such key species that are crucial for ecosystem productivity and stability (Spehn et al. 2002; Temperton et al. 2007; Marquard et al. 2009). However, there is a substantial lack of experimental evidence regarding facilitative legume effects on ANPP of neighboring grassland species under extreme weather conditions. Extreme weather events such as severe drought and heavy rainfall are likely to have strong

effects on vegetation and ecosystem functions like ANPP (Stampfli & Zeiter 2004; Grime et al. 2008; Beierkuhnlein et al. 2011; Dreesen et al. 2012). Such extreme conditions are expected to increase in frequency and magnitude as a consequence of global climate change (Easterling et al. 2000; Jentsch & Beierkuhnlein 2008; IPCC 2012; Rummukainen 2012). Experimental approaches to scrutinize whether impacts of climatic extremes can be modified by plant species richness and community composition have been applied in various grassland ecosystems (e.g. Jentsch et al. 2007; Fay et al. 2008; Smith 2011). However, as yet the potential contribution of legume species to the buffering of ANPP reduction in the face of recurrent, elongated drought or heavy rainfall has not been widely investigated. Under ambient weather conditions, generally all legumes have the ability to fix atmospheric nitrogen via their symbiotic microbial partners (Mosier 2002). Therefore, legumes often do not compete with neighboring plants for soil nitrogen (Paynel et al. 2001), and a surplus of fixed nitrogen can become available when legume plant parts decompose and are mineralized (Tomm et al. 1995). N_2 fixed by legumes can also be transferred to neighboring plants via root exudation (Paynel et al. 2001; Pirhofer-Walzl et al. 2012). Neighboring plants growing close to legumes can benefit from additional nutrient supply (Chu et al. 2004). As a consequence, shoot N uptake, leaf N concentration, $\delta^{15}N$ status, and ANPP of neighboring plants are modified by legume presence (Temperton et al. 2007). Nitrogen fixation and productivity of legumes can be greatly modified at any time during the growing period when soil moisture is inadequate (Striker et al. 2005; Pimratch et al. 2008; Silvente et al. 2012). Symbiotic N_2 fixation by legumes is highly sensitive to water stress or drought as nitrogenase activity depends on the amount of phloem flow into the nodules, which decreases under water stress (Serraj et al. 1999; Marino et al. 2007). Water stress inhibits all aspects of N_2 fixation including nodulation, nodule development, and nodule activity (Serraj et al. 1999; Aranjuelo et al. 2007). On the other hand, soil O_2 concentration is particularly critical to the N_2 fixing function of legumes. An adequate amount of O_2 is required by the rhizobial infected cells to provide energy for N_2 fixation (Witty et al. 1986). Therefore, any reduction in O_2 supply to the nodules under waterlogging condition leads to poor performance of nodulated legumes (Pugh et al. 1995; James & Crawford 1998). In temperate regions some legumes of economic importance such as *Lotus corniculatus* have adapted to grow, nodulate, and fix atmospheric N_2 even under waterlogged conditions (Pugh et al. 1995; James & Crawford 1998; Striker et al. 2005). However, it is necessary to know how legume species perform under annually recurrent pulsed drought and heavy rainfall, which in turn influences their facilitative potential on ANPP of neighboring plant species. In addition, symbiotic N_2 fixation by legumes and above ground biomass production of experimental grassland is reported to steadily increase over at least the first 4 years after community establishment (Mulder et al. 2002; Hooper & Dukes 2004; Roscher et al. 2011). That is why legume facilitation effects on ANPP of neighboring non-legumes may become stronger in the years after community establishment, in particular on N-limited sites. Thus, it is also important to observe how legume facilitation modifies ANPP over time. We compared the responses of legume neighbors and non-legume neighbors in a long term precipitation manipulation experiment during 2007–2010 (EVENT I experiment, Jentsch et al. 2007).

We hypothesized that

(I) legume neighbors would have significantly higher ANPP, higher $\delta^{15}N$ (which is closer to zero), higher leaf N concentration and higher shoot N uptake compared to non-legume neighbors, and that

(II) the effects of legume facilitation on ANPP of neighboring non-legumes increases over time.

(III) Further, we expected that under annually recurrent pulsed drought, legume neighbors would not have significantly higher ANPP, higher $\delta^{15}N$ (which is closer to zero), higher leaf N concentration, and higher shoot N uptake compared to nonlegume neighbors.

(IV) We also hypothesize that under annually recurrent heavy rainfall, legume neighbors would not have significantly higher ANPP, higher $\delta^{15}N$ (which is closer to zero), higher leaf N concentration, and higher shoot N uptake compared to nonlegume neighbors.

Materials and methods

Experimental site

The experiment was set up in the Ecological Botanical Garden of the University of Bayreuth, Germany (49°55′ 19″N, 11°34′55″E, 365 m asl) in the year 2005 and has operated since (Jentsch et al. 2007, 2011). Mean annual temperature of the site is 8.2 °C and mean annual precipitation is 724 mm (1971–2000). Precipitation is distributed bi-modally with a major peak in June-July and a second peak in December-January (data: German Weather Service). The experimental site was built up artificially (about 80 cm in depth) with homogenized sandy subsoil from a nearby quarry. Underlain drainage facilities were installed to avoid soil related heterogeneity. The upper layer (20 cm depth) consisted of homogenized topsoil of the quarry containing higher amounts of organic material. The texture of the soil body is loamy sand (82 % sand, 13 % silt, 5 % clay) with pH(KCl)=4.5 and total N=0.07 % in the upper layer, and with pH(KCl)=6.2 and total N=0.01 % in the lower soil layer.

Experimental design

The EVENT I -experiment has been set up with two fully crossed factors: (i) legume presence versus absence (pair wise comparison of a single mixture of three grassland non-legumes with one legume forb versus the same mixture of three non-legumes with another non-legume forb) and (ii) climate manipulations (control, drought and heavy rainfall). The experimental design consisted of 30 plots, each 2×2 m in size and five replicates of each factorial combination. However, data acquisition was carried out in the central square meter of each plot only in order to avoid edge effects. Plots were blocked pair wise (legume presence versus absence) and randomly assigned within each of the five replications of climate manipulations (control, drought, heavy rainfall). One hundred plant individuals per plot were planted in defined quantitative composition in a systematic hexagonal grid with 20 cm distance between individuals in April 2005. We maintained the composition of originally installed species by regular weeding. Weeds were removed as juveniles and did not produce significant amounts of biomass (and therefore also are considered negligible with regards to competition).

Experimental grassland communities

We investigated two grassland communities, a legume community and a non-legume community, both being composed of four species. We planted three target nonlegumes, the

two common European grasses *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl, *Holcus lanatus* L. and the forb *Plantago lanceolata* L. either together with a legume forb (*Lotus corniculatus* L.), or with a non-legume forb (*Geranium pratense* L.). This substitutive design results in same species number, (initial) density, and (initial) abundances per species of the two communities. *L. corniculatus* and *G. pratense* are perennial, generative and develop similar root systems with persistent taproots that survive over their entire life-span (Klimešová & de Bello 2009; Kutschera et al. 2009). The genet life-span of both species varies between 15 and 30 years. Based on this, we assumed that the legume and its replacement would also be comparable in their productivity and morphology, and thus their competitiveness. However, the legume *L. corniculatus* turned out to be much more productive than its replacement *G. pratense* (see Results). Consequently, the competitive effect of the legume is much higher than that of the forb. Any increased performance (productivity, N-status) of the neighboring target species in the presence of the productive legume as compared to the presence of the unproductive forb can therefore be interpreted as a (strong) indication for a facilitating legume effect. All species used for this experiment were selected with respect to their affiliation to functional groups (grasses, forbs, legume forbs), to life span (perennials), and to their overall importance in nearby and Central European managed grassland ecosystems. Plants used in the experiment were grown from seeds in a greenhouse and even aged when being planted. All plants were acclimated on site since February 2005, reaching heights of approximately 15 cm. Biomass at planting amounted to 0.1–0.6 g dry weight per individual. Data collection for this study started in 2007.

Climate manipulations

The climate treatment involved either annually recurrent pulsed drought or heavy rainfall events in early summer and ambient conditions for control. Intensity of the climate manipulations was based on the local 100-year extreme event in 2007, and then was intensified to the local 1,000-year extreme event during the years 2008– 2010. We determined extremeness of weather treatments by statistical extremity with respect to a historical reference period (extreme value theory), independent of its effects on vegetation (Jentsch 2006). We used the growing seasons (March–September) of 1961–2000 as a reference period (data: German Weather Service). Gumbel I distributions were fitted to the annual extremes, and 100 or 1,000-year recurrent events were calculated. We defined drought as the number of consecutive days without effective precipitation (<1 mm/ day) during the growing season. The control plots remained without climate manipulation throughout the entire period. We maintained drought plots under rain-out shelters during climate manipulations. These were constructed with a steel frame (Hochtunnel, E & R Stolte GmbH, Germany), and covered with a transparent plastic sheet (material: 0.2 mm polyethylene, SPR 5, Hermann Meyer KG, Germany). Rain-out shelters permitted nearly 90%penetration of photosynthetically active radiation. A total of 32 days of drought in 2007 and of 42 days of drought in 2008–2010 was applied in the experiment during the peak growing season in June. Maximum values in the historical data set were 33 days without rain during June and July 1976. We removed the roofs after the experimental drought period. Greenhouse effects due to rain-out shelters were minimized by having an 80 cm clearance between the roof and the ground, allowing for near-surface air exchange. Near-surface air temperature was increased by 1.2 °C during the climate manipulation period. Natural drought periods are usually also accompanied by heat (De Boeck et al. 2010), implying that warming is a realistic scenario for drought periods. We further used artefact controls (irrigating the

amount of natural rainfall under intact rain-out shelters) and did not find significant roof artifacts (Kreyling et al. 2008). We applied heavy rainfall using portable irrigation systems by Veejet 80100 nozzles. Drop size and rainfall intensity resembled natural heavy rainfall events. We manipulated local 100 or 1,000-year heavy rainfall extremes according to extreme value statistics, i.e. 170mm precipitation during 14 days or 260 mm during 21 days, respectively. Maximum values in the historical data set were 152 mm precipitation during 14 days in June 1977. The daily amount of water (around 12.5 mm) was applied in two applications to ensure high soil water saturation. The amount of water added through natural precipitation (if any) was balanced by subtracting the amount of rain from the respective dose. Lateral surface flow was avoided in all plots (control, drought and heavy rainfall) by barriers of plastic sheet pilings around treated plots reaching down to a depth of 10 cm. Soil moisture in the main rooting zone (between 2 and 7 cm depth) was recorded by FD-sensors (Echo.EC- 5／k; Decagon Devices, Pullman,WA, USA). Data were taken from one grassland plot per treatment block in 1-h intervals. Soil moisture content significantly varied between climate manipulations (control, drought and heavy rain; Fig. 1, $F(2, 97)=102.5$, $p<0.0001$). Soil moisture content was lowest during drought and highest during heavy rainfall manipulations. Control plots received only natural precipitation, thus soil moisture content strongly differed between the drought and the heavy rain plots. The year 2008 was extremely dry making the heavy rain manipulation more effective in terms of water supply. Nonetheless, soil moisture values occurred below the wilting point (pF=4.2) for longer periods at the drought plots during climate manipulations in all years.

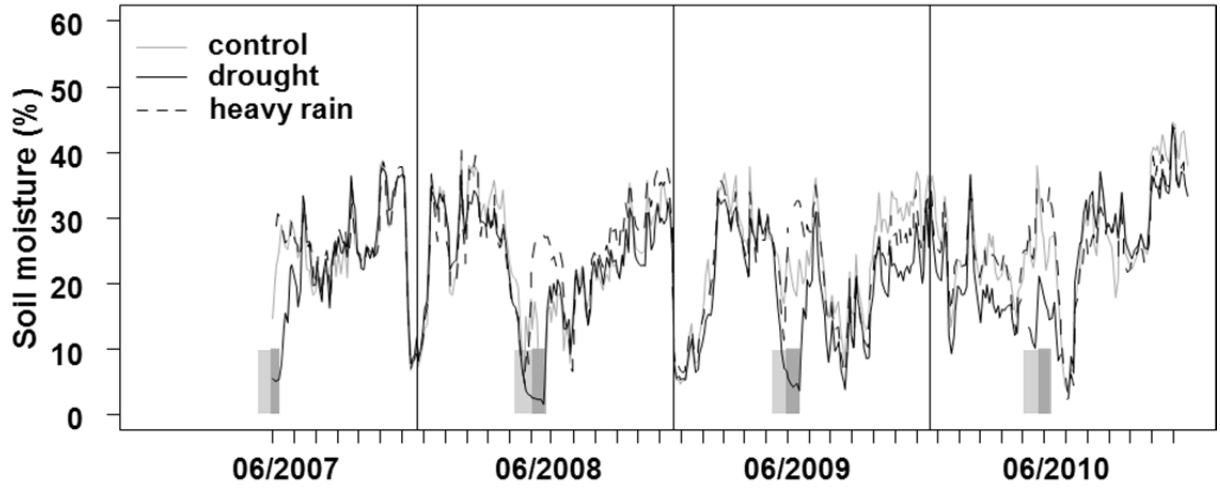

Figure 1 Soil moisture (%) under three weather conditions over time. Soil moisture content was lowest during drought (*light and dark grey boxes*) and highest during heavy rainfall (*dark grey boxes only*) manipulations. Soil moisture content significantly varied among treatments ($F(2, 97) = 102.5$, $p < 0.0001$)

Response parameters

Above-ground biomass production

Standing plant biomass of all target species was harvested twice a year (at the end of climate manipulations in early July and again in mid-September), resembling local agricultural routines. Collected samples were sorted to species and dried to a constant weight at 75 °C and weighed (Ohaus NavigatorTM, Ohaus Corporation, Parsippany, NJ, USA; accuracy±0.01 g). ANPP was calculated as the sum of both harvests per year. Total

ANPP (gm^{-2} year−1) of the three target species *A. elatius, H. lanatus*, and *P. lanceolata* were used for analysis. Biomass data were further used for measuring response ratio, which signified the effect size of legume facilitation (presence and absence) on ANPP of the neighboring target species. The effect size of legume facilitation was calculated by: ln (Legume effect size) = ln (X+Leg/X-Leg), where X+Leg represents the ANPP of the target species in presence of the legume and X-Leg represents the ANPP of the target species in absence of a legume.

Plant nitrogen status

Evidence for legume facilitation related to N_2 fixation was measured by using the $\delta^{15}N$ technique (Högberg 1997; Temperton et al. 2007). The transfer of N_2 from legume species to their neighbors can be tracked via an isotopic signature of $\delta^{15}N$ that is closer to atmospheric $\delta^{15}N$ than N taken up from the soil. Thus, evidence regarding N_2 transfer from legumes to their neighbors can be presented if $\delta^{15}N$ values of legume neighbors are closer to zero compared to non-legume neighbors. Högberg (1997) and Jumpponen et al. (2002) argue that irrespective of legume effect, other mechanisms like $\delta^{15}N$ signal of soil organic matter, species-specific ability of N uptake and plant mixture within the community can also modify the $\delta^{15}N$ status. Here, we used three target species in two plant communities, a legume community and a non-legume community, both having four species. The only difference between the two plant communities was the presence and absence of the legume forb. We replaced the legume forb (*L. corniculatus*) by a non-legume forb (*G. pratense*) and assumed that the altered $\delta^{15}N$ values for the neighboring plants are due to the legume effect rather than other mechanisms. However, the differences in $^{15}N/^{14}N$ ratios between plant-available soil N and N coming from N_2 fixation were small in our study. Therefore, together with $\delta^{15}N$ signals, we also measured legume $\delta^{15}N$, shoot N content and leaf N concentration, as suggested by Högberg (1997), which provides a good way to assess the facilitative effect of legume presence on their neighbors under the three climate treatments. Equally aged south-facing leaves of the target species were collected to determine N-isotope ratios and total leaf N concentrations in July 2007. Leaves were oven dried at 60 °C for 48 h and then fine-milled for analysis. Samples (2.25±0.1 mg)were analyzed using an elemental analyzer (EA 3000; Euro Vector, Italy) coupled online to a ConFlo III interface connected to an isotoperatio mass spectrometer (MAT 253; Thermo Electron). Leaf N concentrations (%) per species per plot were provided by this analysis. Ratio of $^{15}N/^{14}N$ was also reported as the international standard for atmospheric nitrogen. Then $\delta^{15}N$ values were calculated as: $\delta^{15}N$ [‰] = (Rsample/Rstandard) – 1×103, where R represents the ratio of $^{15}N/^{14}N$ isotopes. Shoot N uptake or shoot N content (gm^{-2}) was calculated by multiplying the total above ground dry biomass by the respective leaf N concentration (%). Here, shoot N based on leaf N concentration and total aboveground biomass might result in somewhat wrong absolute values as N concentration varied among plant parts. Leaves always have the highest N concentration, about 4.0– 4.6 % of dry matter content (DM) compared to shoot, stubble and root in the range 2.5–3.5 %, 2– 3 % and 2–2.7 % of DM, respectively (Huss-Danell & Chaia 2005). However, Huss-Danell & Chaia (2005) also suggested that leaves can provide useful indications of N content in shoots and whole plants. Yet we are interested in the relative differences between the treatments in our study and assume that the ratio of N concentration in different plant organs does not differ between treatments.

Soil nitrogen status

Soil nitrogen status was obtained from four homogenized, sieved (< 2 mm), mixed samples of the upper soil layer (between 0 and 10 cm depth) of each plot sampled in July 2008. Plant-available soil nitrogen was extracted using a 1 M KCl solution. After filtration (Typ 15 A Blauband; Roth, Karlsruhe, Germany), nitrate and ammonium concentrations were quantified using flow injection analysis (measurements conducted at BayCEER Analytical Chemistry, Bayreuth, device: FIA-LAB, MLE GmbH, Dresden, Germany).

Statistical analysis

Linear Mixed-Effects Models combined with analysis of variance (ANOVA) were used to test for significant differences between groups at single points of time while taking the split-plot design into account by using block identity as a random factor (e.g., for species-wise analysis of $\delta^{15}N$, shoot N uptake, leaf N concentration and plot wise analysis of soil N status). Species was set as an additional random factor before performing an overall analysis of $\delta^{15}N$ and leaf N concentration. For total shoot N uptake analysis, we summed up the values of our three target grassland species. The fixed factors were legume presence and climate manipulations, which were also tested for their interaction. For time series analyses, Linear Mixed-Effects Models combined with ANOVA were applied to test for the interaction of legume presence and climate manipulations while taking the split-plot design and the repeated measures into account (block identity and time used as random factors). In this case, total ANPP of the three target species were used as response parameter. Homogeneous groups of factor combinations (legume presence, climate manipulations) were identified by Tukey's HSD post hoc comparisons. Prior to statistical analysis, data were ranked (only for shoot N uptake) or square-root or log transformed to improve the homogeneity of variances, or if conditions of normality were not met. All characteristics were tested by examining the residuals versus fitted plots and the normal qq-plots of the linear models (Faraway 2005). Level of significance was set to $p<0.05$. Linear Mixed-Effects Models were conducted with the function 'lme' (package nlme, Pinheiro et al. 2012) and graphs were created using the package sciplot (Morales and R-Development-Core- Team 2012) in R version 2.13.2 (R Development Core Team 2011).

Results

Effects of legume presence irrespective of climate manipulations

Experimental grassland species growing as legume neighbors had significantly higher total ANPP compared to those growing as non-legume neighbors (Total, $F(1, 95)=63.8$, $p<0.0001$; Figs. 2a and 3). Legume neighbors had significantly higher $\delta^{15}N$ values which were closer to zero ($F(1, 68)=4.5$, $p=0.0383$; Table 1), higher leaf N concentration ($F(1, 70)=15.2$, $p=0.0002$; Table 1) and higher shoot N uptake ($F(1, 20)=13.4$, $p= 0.0016$; Fig. 4) compared to non-legume neighbors. The legume effects on $\delta^{15}N$, leaf N concentration, and shoot N uptake were species-specific. $\delta^{15}N$ values of *P. lanceolata* ($F(1,20)=5.5$, $p=0.0292$), leaf N concentration of *A. elatius* and *P. lanceolata* (Arr- $F(1,20)=10.8$, $p=0.0037$; Pla- $F(1,20)=6.3$, $p=0.0211$), and shoot N uptake of *A. elatius* and *H. lanatus* (Arr- $F(1,20)=13.1$, $p=0.0.0017$, Hol- $F(1,20)=8.0$, $p=0.0105$) were significantly promoted by legume presence. Soil N status was higher in the presence of legumes (NH_4^+: $F(1, 19)=4.9$, $p=0.0399$; NO_3^-: $F(1, 19)=1.3$, $p=0.2670$; N%: $F(1, 19)= 4.6$, $p=0.0443$; Fig. 5).

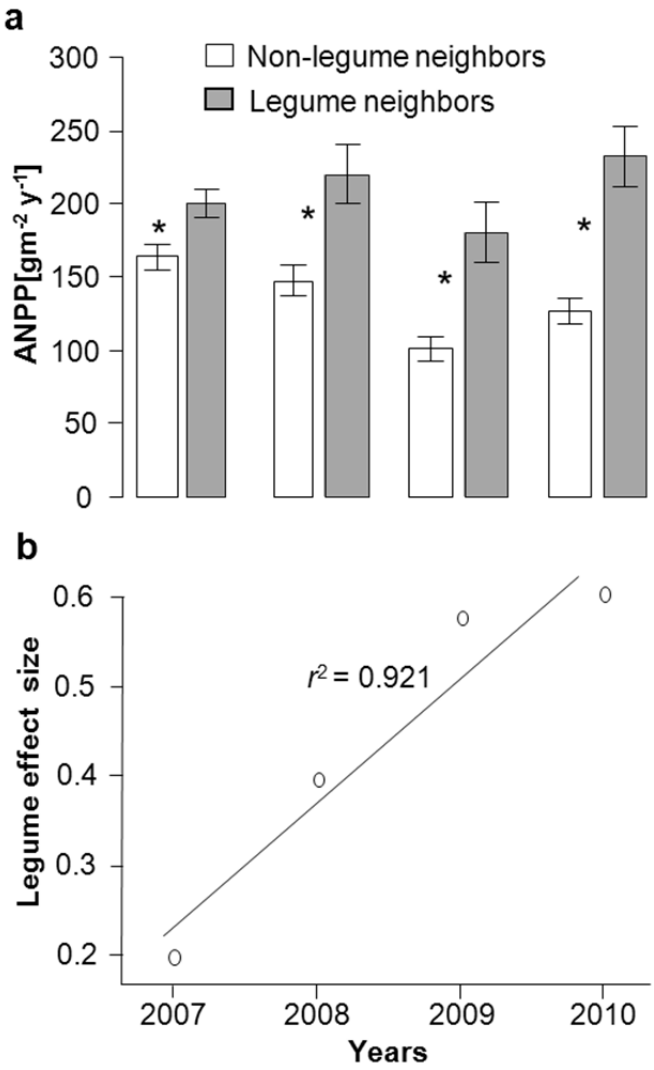

Figure 2 Irrespective of climate manipulations, **a** effect of presence and absence of legume on ANPP and **b** legume effect size over time. Mean values and standard errors of 15 replications are shown. Significant pair wise variation in ANPP due to the presence and absence of legume are marked with asterisks, $p<0.05$. See Materials and method for details about legume effect size

Patterns of legume facilitation effect on ANPP over time

Irrespective of climate manipulations, legume facilitation on ANPP gradually increased over the whole experimental period, 2007–2010 (Linear regression, slope=0.14, r2=0.921; Fig. 2b). This increasing legume facilitation effect was strongest in control (Linear regression: slope=0.18, r2=0.996) and in the heavy rainfall manipulation (slope=0.16, r2=0.736) and effect sizes were smaller for the drought manipulation (slope=0.07, r2=1.000; Fig. 6).

Table 1 Effect of presence (+) and absence (-) of legume on $\delta^{15}N$ and leaf N concentration under three weather conditions (control, drought and heavy rainfall)

Response Parameters	Species	Control		Drought		Heavy rainfall		ANOVA		
		-Legume	+Legume	-Legume	+Legume	-Legume	+Legume	Leg *P*(*F*)	Clim *P*(*F*)	Leg × Clim *P*(*F*)
$\delta^{15}N$	Arr	-2.07 ± 0.1	-1.70 ± 0.76	-2.30 ± 0.97	-1.75 ± 0.53	-2.23 ± 1.88	-2.11 ± 0.95	0.2367(1.5)	0.7121(0.3)	0.8287(0.2)
	Hol	-2.69 ± 1.28	-1.82 ± 0.56	-2.52 ± 1.42	-2.58 ± 1.40	-1.24 ± 1.73	-2.03 ± 1.20	0.7953(0.1)	0.0966(2.7)	0.3012(1.3)
	Pla	-3.65 ± 1.20	-1.55 ± 1.10	-2.49 ± 1.70	-1.72 ± 1.08	-3.47 ± 1.87	-2.84 ± 1.29	**0.0292(5.5)**	0.2476(1.5)	0.4253(0.9)
	Overall[a]	-2.81 ± 1.27	-1.69 ± 0.78	-2.43 ± 1.29	-2.02 ± 1.07	-2.31 ± 1.94	-2.33 ± 1.13	**0.0383(4.5)**	0.9182(0.1)	0.1839(1.7)
Leaf N concentration (%)	Arr	1.87 ± 0.26	2.16 ± 0.27	1.47 ± 0.14	1.97 ± 0.44	1.62 ± 0.34	2.22 ± 0.66	**0.0037(10.8)**	0.2414(1.5)	0.6555(0.4)
	Hol	1.68 ± 0.21	1.76 ± 0.06	1.18 ± 0.07	1.29 ± 0.14	1.81 ± 0.27	1.94 ± 0.29	0.1411(2.3)	**<0.0001(29.7**)	0.9676(0.0)
	Pla	1.10 ± 0.21	1.40 ± 0.24	1.09 ± 0.23	1.39 ± 0.35	1.04 ± 0.16	1.11 ± 0.35	**0.0211(6.3)**	0.2227(1.6)	0.5187(0.7)
	Overall[a]	1.55 ± 0.40	1.77 ± 0.38	1.25 ± 0.22	1.55 ± 0.44	1.49 ± 0.42	1.76 ± 0.65	**0.0002(15.2)**	**0.0050(5.7)**	0.8947(0.1)

Mean values and standard deviations for five replications are shown here. Significant (ANOVA, $p < 0.05$) results are set bold

[a]block and species were used as random factor for overall analysis

Effects of legume presence under drought

Under annually recurrent drought conditions, total ANPP of the three target species was not affected by legume presence (significant interaction between climate and legume treatment; post-hoc test of the legume effect for drought only: p=0.1246; Fig. 3). Similarly, the effects of legume presence on ANPP were not significant for *H. lanatus*, and *P. lanceolata* (again significant interaction between climate and legume treatment; posthoc test of the legume effect for drought only: Hol, p= 0.3243; Pla, p=0.9999; Fig. 3). The overall legume effects were not modified by the interaction of climate manipulations for *A. elatius*, implying that this target species was facilitated by legume presence also under drought (interaction between climate and legume treatment, p=0.4090; Fig. 3). Irrespective of the legume effect, total ANPP of all target species was not significantly affected by the drought manipulation. The effects of legume presence on $\delta^{15}N$, leaf N concentration, and shoot N uptake over all species were not altered by the interaction between climate and legume treatments and therefore persisted also under drought conditions (Table 1, Fig. 4). But, both legume and non-legume neighbors grown under drought conditions showed a tendency for lower leaf N concentrations compared to those plants grown under control conditions (Climate, $F(2,70)=5.7$, p=0.0050, Table 1; Control versus Drought, p=0.0572). Shoot N uptake significantly varied between climate manipulations ($F(2,20)=3.6$, p=0.0468) and it was slightly lower under drought compared to control (Fig. 4). At the species level, leaf N concentration and shoot N uptake of *H. lanatus* were significantly lower under drought conditions compared to control (Control versus drought: Leaf N concentration, p<0.0001, Shoot N uptake, p=0.0053; Legume neighbors under control versus legume neighbors under drought: Leaf N concentration, p=0.0098, Shoot N uptake, p=0.0536). The significant legume effects on $\delta^{15}N$ in *P. lanceolata* and leaf N concentration in *A. elatius* and *P. lanceolata* were not affected by the climate manipulations (Table 1). Likewise, the legume effect on N-uptake of *A. elatius* and *H. lanatus* also persisted under drought conditions (Fig. 4). Among the three response parameters of soil N status (NH_4^+, NO_3^- and N %) only soil NH_4^+ significantly varied between climate manipulations (Climate, $F(2, 19)=3.8$, p=0.0422). Soil NH_4^+ and soil N% furthermore showed positive legume effects irrespective of climate manipulations (Fig. 5).

Effects of legume presence under heavy rainfall

Total ANPP of the three target species was positively affected by legume presence under heavy rainfall conditions (significant interaction between climate and legume treatment; post-hoc test of the legume effect for heavy rainfall only: p<0.0001; Fig. 3). This pattern was mainly driven by *P. lanceolata*, which showed a significant positive legume effect only under heavy rainfall (post-hoc test of the legume effect for heavy rainfall: p=0.0024, Fig. 3). ANPP of *H. lanatus* was not facilitated under heavy rainfall, while ANPP of *A. elatius* was persistently facilitated by legume presence also under heavy rainfall (significant main effect but no significant interaction with climate manipulations, Fig. 3). In addition, irrespective of legume effects, heavy rainfall significantly increased total ANPP of the target species by 18 % compared to control (p=0.0317). Leaf N concentration was also significantly impacted by the climate manipulations ($F(2,70)=5.7$, p=0.0050, Table 1), and under heavy rainfall it was slightly higher in legume neighbors (1.76±0.65) compared to non-legume neighbors (1.49±0.42). At the species level, leaf N concentration of *H. lanatus* was significantly higher under heavy rainfall compared to drought (Heavy rainfall versus Drought, p<0.0001; Legume neighbor under heavy rain versus legume neighbor under drought, p=0.0002). The significant legume effects of overall δ15N, total shoot N uptake, individual N-uptake of *A. elatius* and

H. lanatus, and soil NH_4^+ persisted under the heavy rainfall manipulation (Table 1, and Figs. 4 and 5). In addition, heavy rainfall had no significant effect on soil N status (Fig. 5).

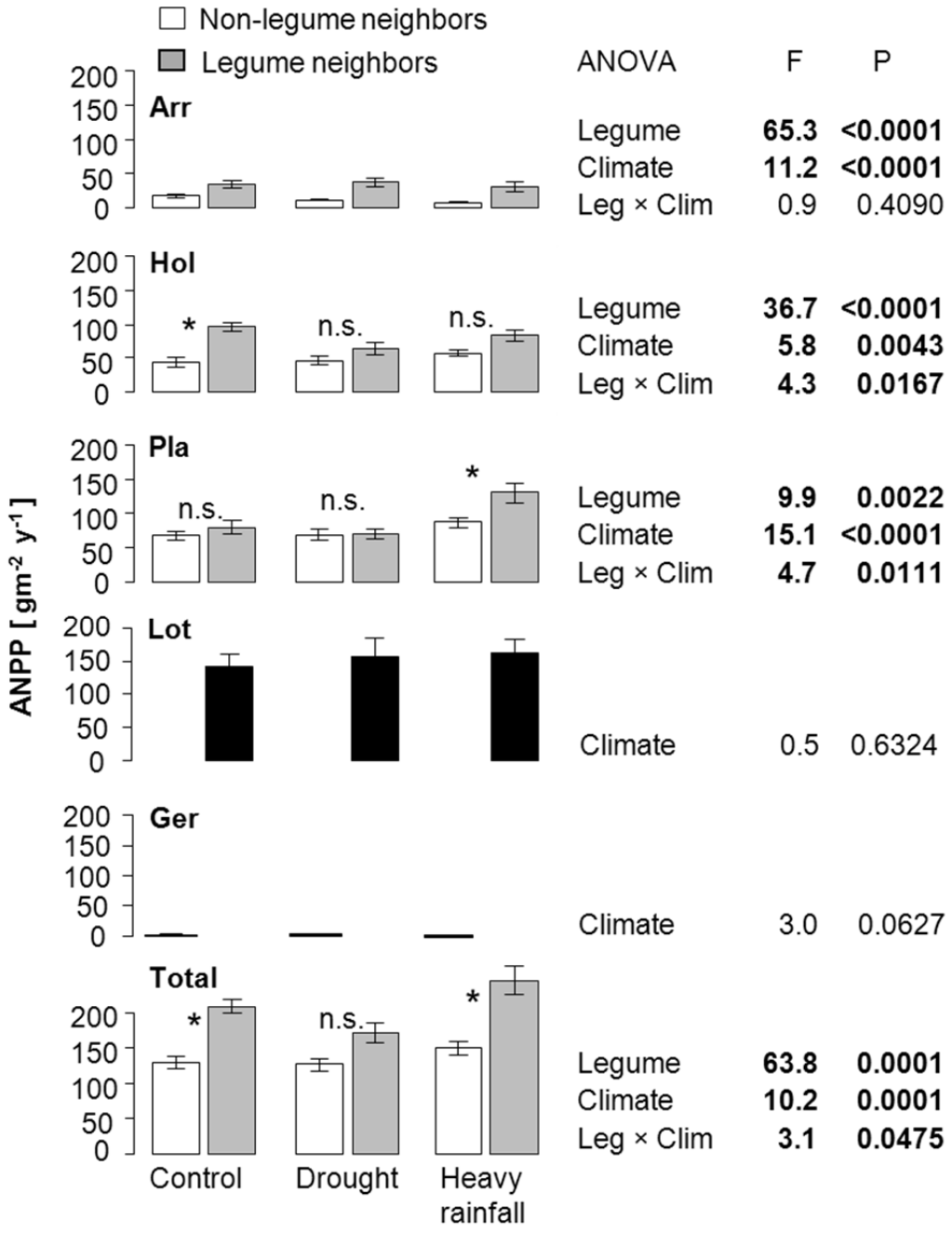

Figure 3 Legume effect on ANPP under three experimental climatic conditions (control, drought and heavy rainfall). Mean values and standard errors of five replications over 4 years (2007–2010) are shown as the sum of two harvests per year. Significant variations are marked in bold ($p<0.05$) and significant pair wise comparisons are indicated by asterisk (Tukey's post-hoc, $p<0.05$) in case of significant interactions between legume presence and climate manipulations. ANPP of three target species (Arr, Hol, and Pla) were summed up (Total)

Discussion

Effects of legume presence irrespective of climate manipulations

We confirmed the first hypothesis that target species will profit from legume presence as indicated by increased ANPP, higher $\delta^{15}N$, higher leaf N concentration, and higher shoot N uptake compared to non-legume neighbors (Table 1, Figs. 2a, 3 and 4). Concerning isotopic signature of $\delta^{15}N$, leaf N concentration, and shoot N uptake, responses of the three target species to legume presence were found to be species-specific (Table 1 and Fig. 4). $\delta^{15}N$ values of *P. lanceolata* significantly depended on legume presence but the $\delta^{15}N$ values of the other two target species, *A. elatius* and *H. lanatus*, were not significantly modified by legume presence. Along with *P. lanceolata*, leaf N concentration of *A. elatius* benefited from legume presence. Furthermore, legume presence had a significant effect on shoot N uptake of *A. elatius* and *H. lanatus*, yet shoot N uptake of *P. lanceolata* did not significantly vary with legume presence. Soil N status data confirmed that the legume presence had beneficial effects on soil NH_4^+ and N% (Fig. 5).

Comparable positive effects of legume presence on nutrient availability, uptake, and growth of neighboring species are reported from many other studies (e.g. Tomm et al. 1995; Høgh-Jensen & Schjoerring 2000; Paynel et al. 2001; Spehn et al. 2002; Chu et al. 2004; Temperton et al. 2007; Marquard et al. 2009; von Felten et al. 2009; Küchenmeister et al. 2012; Pirhofer-Walzl et al. 2012; Roscher et al. 2012). This underlines that legumes play a crucial role for the performance of grasslands by supporting the fixation of atmospheric N_2 which becomes available for the whole plant community. Apparently, legume presence also reduces the competition for soil N ("nitrogen sparing") as legumes rely more on atmospheric N_2 than on soil N. However, our study provides novel insights by demonstrating species-specific responses to legume presence, i.e. species-specific facilitation.

We used a substitutive design where the legume *L. corniculatus* was replaced by a non-legume forb, *G. pratense*. Despite *L. corniculatus* being much more productive than *G. pratense* (Fig. 3), and thus probably competing more with the neighboring species for above and below ground resources, legume presence promoted the growth and N uptake of its neighbors via N sparing (Temperton et al. 2007; von Felten et al. 2009) or N transfer (Høgh-Jensen & Schjoerring 2000; Pirhofer- Walzl et al. 2012). Based on this, the true legume effect in our study might even exceed the observed facilitation. In addition, overall $\delta^{15}N$ values, leaf N concentration, shoot N uptake data of legume neighbors, and the legume species itself also support facilitation by the legume via N sparing or transfer, i.e. a legume effect. Thus, we conclude that the positive responses of neighboring non-legumes are due to legume facilitation rather than species-identity effects on competitive balance.

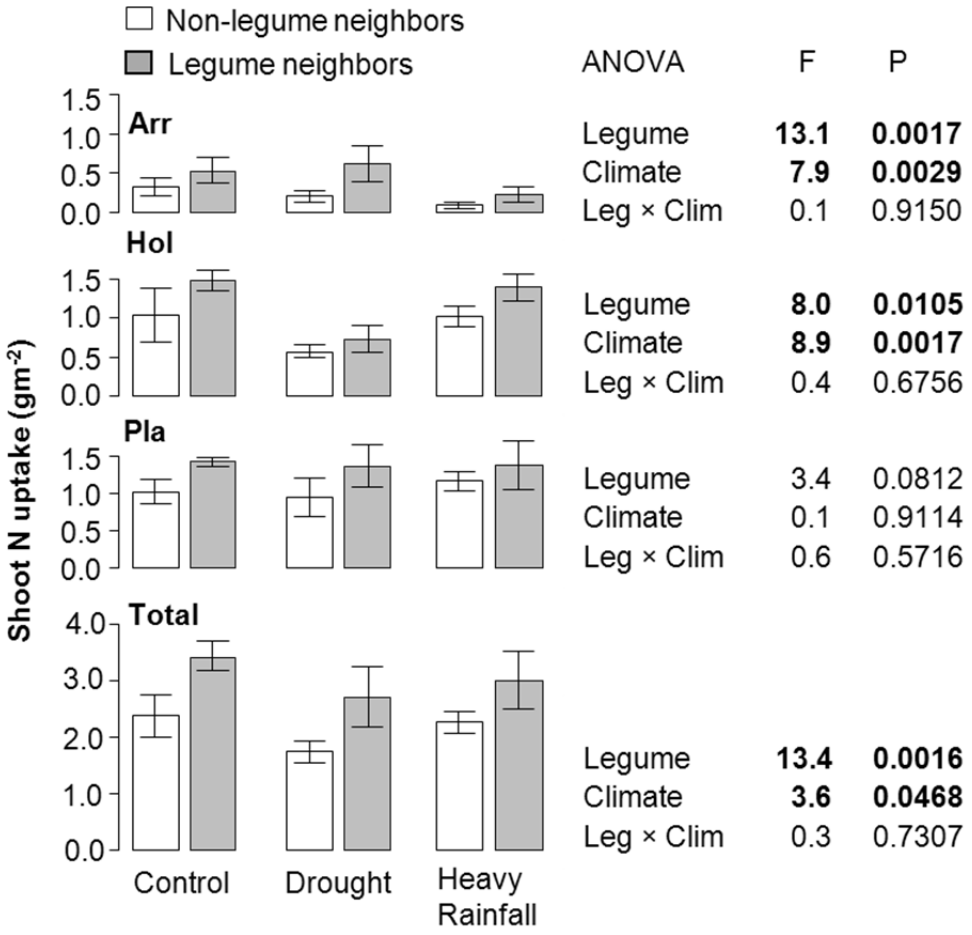

Figure 4 Effect of legume presence and absence on N uptake under three climate conditions (data from 2007). Significant variations are marked in bold ($p<0.05$). Legume presence and climate manipulations had significant effect on total N uptake. N uptakes of three target species (Arr, Hol and Pla) were summed up (Total)

Patterns of legume facilitation effect on ANPP over time

We confirmed the second hypothesis that legume facilitation on ANPP of neighboring non-legumes increases over time. This significant effect was observed under control and heavy rain conditions (Fig. 6). The positive influence of legumes under drought also gradually increased with time, yet with a much smaller effect size (slope=0.07). On sandy soils, productivity of temperate grasslands was found to be limited by N availability (Semmartin et al. 2007; Yu et al. 2009). Increasing importance of facilitation by legumes in the present study points towards a self-enforcing feedback of legume facilitation, which might be caused by increasingly efficient N-fixation in an N-poor sandy soil substrate. Roscher et al. (2011) reported increasing amount of N_2 fixation by legumes over 4 years after their establishment. Progressively positive legume effects on neighboring species over 5 years were observed by Marquard et al. (2009). Mulder et al. (2002) found less strong legume effects, but are also suggesting that legume presence contributes towards greater biomass and total nitrogen over the first three years in experimental grassland. However, most previous experiments were installed by sowing and thus could not investigate neighborhood effects between equally spaced individuals but only the overall performance of communities.

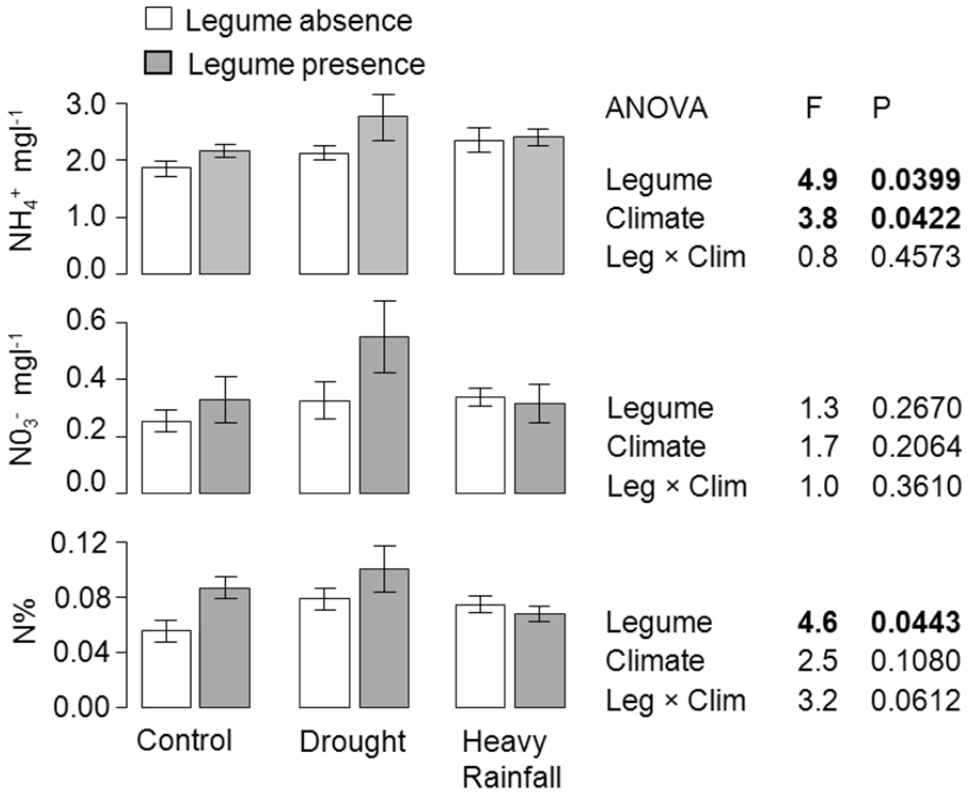

Figure 5 Effect of presence and absence of legume on soil N status (NH_4^+, NO_3^- and N %) under three climate conditions (data from 2008). Significant results ($p<0.05$) are marked in bold

Effects of legume presence under drought

The third hypothesis that under annually recurrent drought legume neighbors would not have significantly higher ANPP, higher $\delta^{15}N$, higher leaf N concentration, and higher shoot N uptake compared to non-legume neighbors, was only partly supported by the experiment. Facilitation of total ANPP of the three target species and of species specific ANPP of two of the three target species disappeared under drought conditions (Fig. 3). However, positive effects of legume presence found under control conditions persisted under drought conditions for ANPP of A. elatius, $\delta^{15}N$ of *P. lanceolata*, leaf N-concentrations, N-uptake, soil NH_4^+, and soil N% (Figs. 3, 4, and 5, and Table 1). Possible reasons behind this reduced facilitation of growth can be either a reduction in N_2 fixation by legumes or an inhibition of N uptake due to the water stress; but also to the interaction of both mechanisms. Astonishingly, compared to the controls drought had no significant negative effect on total ANPP of our three target species. Drought was found to initiate plant physiological processes that can stabilize biomass production and this may regulate ecosystem productivity (Jentsch et al. 2011). Under drought, the positive legume effect on growth of the target species disappeared. This pattern could be explained by reduced N_2 fixation by legumes under drought. Serraj et al. (1999) showed the sensitivity of N_2 fixation to drought via impacts on nitrogenase activity, which depends on quantitative phloem flow into the nodules. Thus, any variation in phloem flow as a result of changes in turgor pressure in the leaf is likely to cause a change in nodule activity, which ultimately reduces of N_2 fixation under drought.

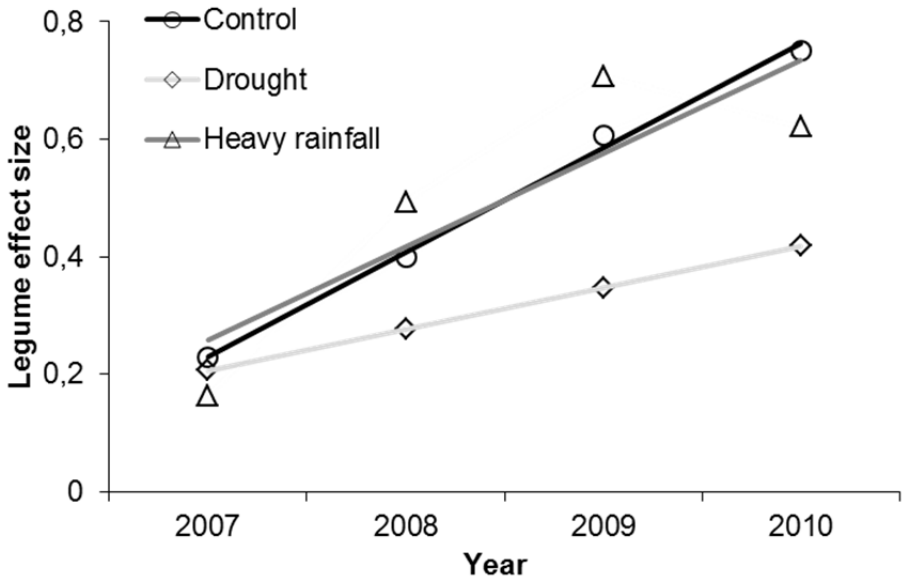

Figure 6 Legume effect size under control, drought and heavy rainfall gradually increases over time. Linear regression: control (*black line*), slope=0.18, r^2=0.996; drought (*light grey line*), slope=0.07, r^2=1.000; and heavy rainfall (*dark grey line*), slope=0.16, r^2=0.736 (See method for details about legume effect size)

In our experiment though, N_2 fixation by the legumes appeared not to be impaired in the drought plots, as indicated by the unaffected $\delta^{15}N$, shoot N content, and leaf N concentration of the legume species itself (Fig. 7). Besides, we observed slightly higher soil N-concentrations in the drought plots. Here, we applied pulsed stress events and as a result could not detect if N_2 fixation had taken place during the peak of the drought treatment, as it could have occurred before and after the treatment. In addition, it is possible that higher soil N-concentrations observed in drought treatments could be driven by decaying roots after short-term partial die-back.

The lower leaf N concentration of both legume and non-legume neighbors grown under drought compared to those grown under control conditions emphasizes the limitation in N uptake by drought. At the species level, *H. lanatus* showed that leaf N concentration and shoot N uptake were significantly lower under drought conditions compared to control and legume presence could not compensate this reduced uptake (Table 1). A recent study found that N uptake efficiency is an important trait to support growth under drought (Weih et al. 2011). Abdelhamid et al. (2011a) found that dry surface soil causes reduction in shoot N uptake through reduction in N_2 fixation. Although the overall reduction of the legume effect under drought has already been documented, our study differs from previous approaches (Serraj et al. 1999; Sadale & Karadge 2010; Abdelhamid et al. 2011b; Nawaz et al. 2012) as well in the systematic design as according to the relevant mechanism by pointing at the N uptake (Abdelhamid et al. 2011a; Van den Berge et al. 2011) to be more sensitive to drought than N_2 fixation. Our reduced N-uptake results can be explained by limited diffusion of nutrients from the soil matrix to the absorbing root surface during low soil moisture (Hu et al. 2007). Consecutively, nutrient transport from the roots to the shoots decreases due to reduced transpiration rates (Duman 2012). Drought in our experiment was applied in forms of recurring pulsed stress events. Neighboring plants did not compensate the reduced uptake

during the drought, although conditions before and after the drought manipulation allowed for N-uptake. In sum, the present study indicates that facilitation by a legume species is reduced under annually recurrent pulsed drought events as a consequence of reduced N-uptake rather than N_2 fixation.

Facilitation of growth by legume presence was differently affected by the drought manipulation for our three target species: *H. lanatus* was facilitated only under control conditions, *P. lanceolata* was facilitated only under heavy rainfall, and *A. elatius* was facilitated irrespective of climate manipulations. The species differ in their rooting system with *P. lanceolata* being characterized by its persistent taproot system (similar to *L. corniculatus*, Klimešová & de Bello 2009) reaching deep into the soil and potentially providing an advantage compared to the shallow-rooted *H. lanatus* (Kutschera et al. 2009) in taking up N which is leached downward due to heavy rainfall and accompanied excess of water. Similarly, *A. elatius* is a species rooting deeper than *H. lanatus* (Kutschera et al. 2009), while both are graminoids with dense, fibrous root system potentially being beneficial in comparison to *P. lanceolata* in the absence of excess water moving downward. The main message beyond this speculative explanation, however, is that facilitation under altered climatic conditions is highly species-specific. The three target species in our study showed complementary patterns, this finding can be linked to an overall buffering effect of biodiversity on ecosystem functioning in the face of perturbation (here extremes), as expected by the insurance hypothesis (Yachi & Loreau 1999).

Effects of legume presence under heavy rainfall

We finally hypothesized that under annually recurrent heavy rainfall legume neighbors would not exhibit significantly higher ANPP, higher $\delta^{15}N$, higher leaf N concentration, and higher shoot N uptake compared to non-legume neighbors. This expectation was partially confirmed by our results (Table 1, Figs. 3 and 4). The total ANPP significantly increased with legume presence under heavy rainfall, while the corresponding values of $\delta^{15}N$, leaf N concentration, and shoot N uptake did not show significant changes. A positive growth effect with increased precipitation can be either caused by increased N_2 fixation or by higher soil moisture and thus more nutrient uptake; but again it can also be a consequence of the interaction of both mechanisms. Previous studies indicated that increased precipitation has positive effects on ANPP of grasslands (Sala et al. 1988; Yang et al. 2008), but such effects depend strongly on the regional climate and ecosystem. Temperate managed grasslands (e.g. hay meadows) cannot be directly compared to continental natural prairies. It is evident that adequate soil moisture supports N_2 fixation (Abdelhamid et al. 2011a; Singh et al. 2011). Some legume species (i.e. *L. corniculatus*) can fix atmospheric N_2 even under waterlogged conditions when soil O_2 concentration becomes low (Witty et al. 1986; Pugh et al. 1995; James & Crawford 1998; Striker et al. 2005). Although our heavy rain treatment had gone beyond field capacity towards water saturation (Fig. 1), the $\delta^{15}N$ signature, shoot N content, and leaf N concentration of the legume species (*L. corniculatus*) did not differ significantly when comparing the heavy rainfall treatment with the control and the drought treatment. Besides, the interaction of legume presence and heavy rainfall had

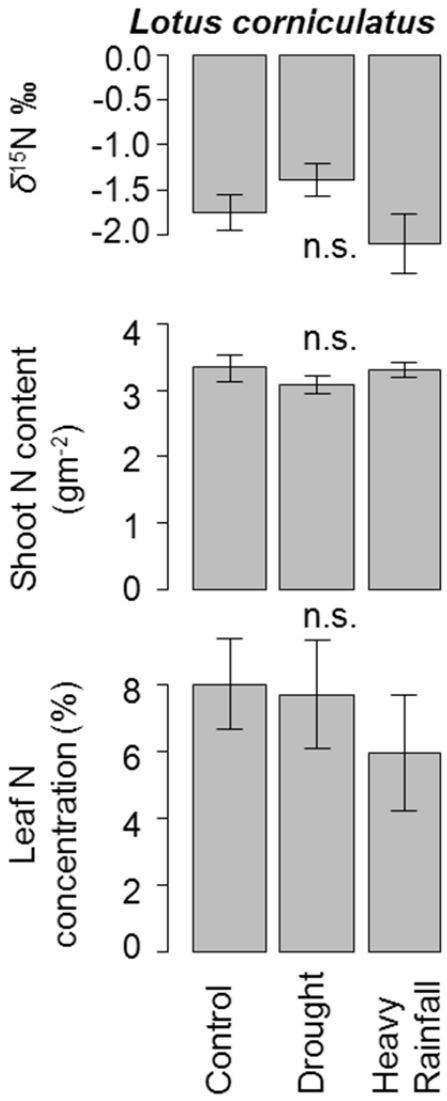

Figure 7 Effect of climate manipulations on $\delta^{15}N$, shoot N content, and leaf N concentration of the legume *L. corniculatus* (data from 2007). Data from five replications are shown

no significant effect on soil N status. Therefore, no evidence of higher N_2 fixation was found under heavy rain (Fig. 7). Increased N uptake or leaching under heavy rainfall could explain the absence of this response. Overall leaf N concentrations of legume neighbors were slightly higher under heavy rainfall compared to nonlegume neighbors, indicating a beneficial effect of legume presence. The leaf N concentration of *H. lanatus* clearly reflected this beneficial effect. Unfortunately, our study cannot provide evidence for nitrogen leaching, but, it was found that a considerable amount of nitrogen losses can take place under low species diversity (Scherer-Lorenzen et al. 2003), which we also have in the present study. Scherer-Lorenzen et al. (2003) observed increased leaching of nitrate in legume plots compared to non-legume plots. Here, we used a soil which is highly permeable. This soil type may have allowed leaching under heavy rain conditions. A previous study found that soil N leaching is associated with both heavy rainfall and soil type (Rimski-Korsakov et al. 2004). In the latter study, heavy rainfall even caused the leaching of previously accumulated soil nitrate. Therefore, it is possible that N_2 fixation may be enhanced in heavy rain plots, but this enrichment is not reflected in the plants because soil nitrogen is leached to the aquifer.

Conclusions

Legumes facilitated the productivity of neighboring plant species in experimental temperate grasslands. However, the positive legume effects on growth disappeared under extreme drought conditions and were generally species-specific in their response to climate manipulations. These findings additionally emphasize the importance of legume presence and species-specific traits or complementarity of species for maintaining a stable productivity in the face of altered climatic conditions.

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Manuscript 6

Toward a better integration of biological data from precipitation manipulation experiments into Earth system models

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Toward a better integration of biological data from precipitation manipulation experiments into Earth system models

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Abstract

The biological responses to precipitation within the terrestrial components of Earth system models, or land surface models (LSMs), are mechanistically simple and poorly constrained, leaving projections of terrestrial ecosystem functioning and feedbacks to climate change uncertain. A number of field experiments have been conducted or are underway to test how changing precipitation will affect terrestrial ecosystems. Results from these experiments have the potential to vastly improve modeled processes. However, the transformation of experimental results into model improvements still represents a grand challenge. Here we review the current state of precipitation manipulation experiments and the precipitation responses of biological processes in LSMs to explore how these experiments can help improve model realism. First, we discuss contemporary precipitation projections and then review the structure and function of current-generation LSMs. We then examine different experimental designs and discuss basic variables that, if measured, would increase a field experiment's usefulness in a modeling context. Next, we compare biological processes commonly measured in the field with their model analogs and find that, in many cases, the way these processes are measured in the field is not compatible with the way they are represented in LSMs, an effect that hinders model development. We then discuss the challenge of scaling from the plot to the globe. Finally, we provide a series of recommendations aimed to improve the connectivity between experiments and LSMs and conclude that studies designed from the perspective of researchers in both communities will provide the greatest benefit to the broader global change community.

1 Introduction

Current and projected shifts in precipitation have the potential to impact vital terrestrial ecosystem functions including worldwide food production, carbon storage, and patterns of biodiversity loss (Weltzin et al. 2003). Precipitation is a primary driver of cellular- (e.g. Rodgers et al. 2012), individual- (e.g. Hanson et al. 2001), population- (e.g. Avolio et al.

2012), community- (e.g. Kulmatiski & Beard 2013), and ecosystem-scale (e.g. Suseela & Dukes 2012) processes across a variety of temporal scales (Figure 1).

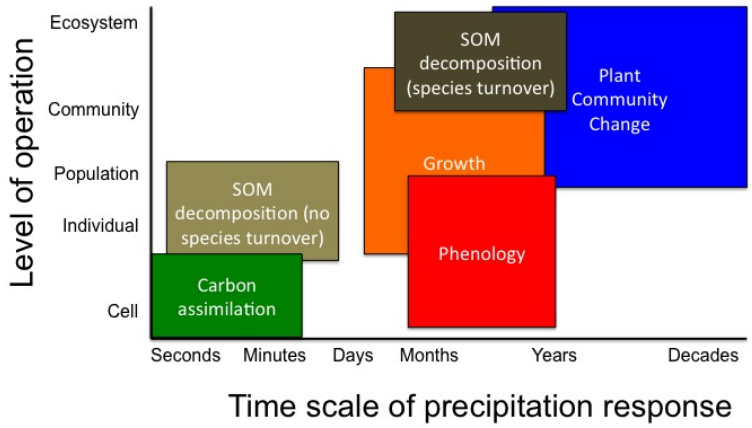

Figure 1 Conceptual graph of the physical (y-axis) and temporal (x-axis) scales of operation of the different processes discussed in the review. The scale of operation will determine the influence of a given precipitation change on each response. Researchers need to keep these scales in mind when evaluating and quantifying biological response to precipitation

These processes are affected by both total precipitation (Wu et al. 2011) and variation in the timing of precipitation, including intraannual (Grant et al. 2014; Peñuelas et al. 2004; Reichstein et al. 2013; Reyer et al. 2012) and interannual (Fatichi & Ivanov 2014; Hsu et al. 2012; Knapp & Smith 2001; Peñuelas et al. 2004) variabilities. In light of the projected changes in global precipitation patterns (Intergovernmental Panel on Climate Change (IPCC) 2012, 2013; Sillmann et al. 2013), there is a critical need to understand how changes in precipitation can impact terrestrial ecosystems. One way to examine these processes in the field is through the use of precipitation manipulation experiments. The design and implementation (Beier et al. 2012; Hanson 2000; Miranda et al. 2011) as well as results (Reyer et al. 2012; Wu et al. 2011) from these experiments have been recently reviewed. However, there is a need for a continued effort to integrate the results of field experiments into the land surface models (LSMs) that simulate the response of the terrestrial biosphere to climate forcing in the context of Earth system models (ESMs) (e.g. Collins et al. 2011) used to project rates and impacts of future climate change. Currently, LSM representation of many biological responses to precipitation is mechanistically simple and/or poorly constrained due to lack of appropriate parameterizations for many ecosystems (Powell et al. 2013; Todd-Brown et al. 2013). This reflects both the limited empirical data necessary to improve models and a lack of comparisons between model simulations and observational data. In this review, we outline ways that precipitation manipulation experiments can be designed to help inform models and, ultimately, improve model realism for global change studies. Through collaboration with the modeling community, the applicability of plot-scale results could be greatly enhanced. Although this idea has been discussed before (Beier et al. 2012; Classen & Langley 2005; Dietze et al. 2013), the transformation of experimental results into model improvements is still fragmentary. This review is designed to provide a framework to bridge the gap between these two communities and to reignite the efforts necessary for interdisciplinary collaborations. Here we first review the most recent projections for future terrestrial precipitation (i.e. Coupled Model Intercomparison Project phase 5; section 2) and

follow this with a brief review of the structure and functioning of current-generation LSMs (section 3). In section 4, we explore the different approaches taken to evaluate the response of terrestrial ecosystems to precipitation in the field. We not only focus on the efficacy of different experimental designs for informing LSMs but also allude to natural experiments that are useful for informing LSMs. In section 5, we highlight routine measurements, including hydrological and meteorological measurements that, if taken, would aid the incorporation of more sophisticated data into models. We then investigate the representation of some precipitation responses in LSMs and examine how similar responses are measured in the field using four commonly measured biological processes as examples: (1) carbon assimilation and productivity, (2) phenology, (3) soil organic matter (SOM) decomposition, and (4) plant community dynamics (section 6). We provide recommendations for how measurements of these processes could be made in a way that is useful for model development. Finally, as this review considers a connection between plot-scale data and global-scale models, we describe ways to improve model-data connectivity (i.e. the ability of experimental data to evaluate and improve models) through the use of targeted observational data (section 7). We conclude that, by following a few simple recommendations, the applicability of field experiments and realism of LSMs could be greatly enhanced (section 8).

2 Future Terrestrial Precipitation Change

Increasing global surface temperatures are expected to enhance rates of evaporation and precipitation, over both land and the ocean (Allan et al. 2013; Held & Soden 2006; Schneider et al. 2010). Contemporary Coupled Model Intercomparison Project (CMIP) analyses suggest that the global mean wet-day precipitation (total precipitation on days where precipitation is >1 mm) will increase 3.5–9%, with projected totals increasing under more intense radiative forcing scenarios. However, regional changes in mean precipitation are projected to differ, with amounts increasing in some locations (e.g. high northern latitudes and in Eastern Africa, South and Southeast Asia, and Antarctica) and decreasing in others (e.g. Central America, South Africa, and the Mediterranean) (Sillmann et al. 2013). These regional effects are expected not only as a result of climate change but also as a result of rapid land use and land cover change underway globally (Pielke et al. 2011).

In concert with altered mean precipitation, models also project an increase in the frequency and intensity of extreme precipitation events (O'Gorman 2012; O'Gorman & Schneider 2009; Sillmann et al. 2013; Tebaldi et al. 2006) and an increase in precipitation variability with more frequent droughts and floods (Easterling et al. 2000; IPCC 2012, 2013). Observations suggest that these changes are already occurring (Min et al. 2011), with North America showing a strong increase in extreme precipitation events (Alexander et al. 2006). An increase in these events is projected to occur globally, even in areas of the world where total precipitation is projected to remain unchanged or decrease (Sillmann et al. 2013). However, while projections of extreme precipitation events over large areas (i.e. the continental scale) are robust, more local projections may be masked by internal climate variability (Fischer et al. 2013). Precipitation is an important forcing that governs hydrology, which in turn affects not only energy and water cycles but also biological processes. As such, models need to simulate the response of these processes to a range of precipitation magnitudes and intensities. A large body of research has been devoted to understanding and properly simulating these responses (Cao & Woodward, 1998; Katul et al. 2007; Knapp et al. 2008; Weltzin et al. 2003). However, a greater understanding of the mechanisms driving biological

responses to precipitation changes and consequent feedbacks is needed to ensure better and more reliable future projections.

3 Current-Generation LSMs

In the simplest form, a LSM provides boundary conditions for computing momentum, energy, and mass (water, carbon) fluxes at the interface between the land surface and the atmospheric boundary layer. We use the term LSM generically, including LSM sensu stricto and LSMs embedded in ecohydrological, biogeochemical, and dynamic vegetation models, but we mostly focus on large-scale applications in the context of ESMs and long-term studies. LSMs have evolved greatly (see Sellers et al. 1997; Pitman 2003), beginning as simple single soil layer, implicit vegetation models in the late 1960s (Manabe, 1969), and expanding to include multiple soil layers and explicit vegetation in the late 1970s and 1980s (Deardorff, 1978; Dickinson et al. 1993, 1986; Entekhabi & Eagleson, 1989; Noilhan & Planton, 1989; Sellers et al. 1986; Verseghy, 1991), carbon assimilation in the early 1990s (Bonan, 1995; Cox et al. 1998; Sellers et al. 1992, 1996), and finally, most currently, different plant types (Bonan et al. 2002) and dynamic changes in carbon pools and vegetation properties (Bonan et al. 2003; Clark et al. 2011; Dickinson et al. 1998; Krinner et al. 2005) as well as dynamic nitrogen pools (Dickinson et al. 2002; Thornton et al. 2009; Zaehle & Friend 2010). LSMs have been developed and applied at different scales, and while there is no clear guidance for the scale at which a particular LSM should be applied, the tendency is to go toward finer spatial scales and to validate LSMs at the scale of flux tower footprints (e.g. 1000–10,000m2) (e.g. Blyth et al. 2010). However, components that constitute the land surface schemes of climate models and ESMs (e.g. Best et al. 2011; Clark et al. 2011; Krinner et al. 2005; Lawrence et al. 2011; Medvigy et al. 2009; Niu et al. 2011; Noilhan & Mahfouf, 1996; Oleson et al. 2010; Viterbo & Beljaars, 1995) typically operate at larger spatial scales from tens to thousands of kilometers and temporal scales from minutes to days and beyond. These models are continually adding potentially relevant biological responses to precipitation and hydrological changes, often as a function of soil moisture (section 5). Nonetheless, the functions used are often empirical, relying on generalized responses and omit the driving biological processes. Although these functions may simulate historical data well (Kleidon & Heimann, 1998; Porporato et al. 2002), the omission of driving mechanisms decreases the reliability of future projections. Unfortunately, the reliance on empirical models is a necessity due to limited understanding of responses of biological processes in the field (Arneth et al. 2010). In the sections below, we consider how precipitation manipulation experiments, which are fundamentally designed to characterize these processes, can help decrease the uncertainty associated with precipitation responses in LSMs. As stated above, we focus primarily on LSMs that constitute, or are designed for, the land surface schemes of climate models and ESMs (e.g. Best et al. 2011; Clark et al. 2011; Krinner et al. 2005; Lawrence et al. 2011; Oleson et al. 2010; Raddatz et al. 2007; Shevliakova et al. 2009; Sitch et al. 2003; Zaehle & Friend 2010). However, the discussion is also relevant for mechanistic ecohydrological models (e.g. Fatichi et al. 2012b; Ivanov et al. 2008b), which are typically applied at smaller spatial scales and could provide a bridge for improving large-scale models.

4 Field Studies of Biological Responses to Precipitation Changes

Field studies have been underway that manipulate precipitation over small areas (i.e. plots) in order to examine terrestrial responses to future precipitation change (Figure 2). Plot sizes vary greatly between experiments, ranging from tens (e.g. Beier et al. 2004) to hundreds (e.g. Lamersdorf et al. 1998) to thousands (e.g. Hanson et al. 2003; Pangle et al. 2012) of square meters but are typically smaller than the area simulated by common LSM applications (section 3). Plots are typically equipped with instrumentation to monitor soil moisture and meteorological variables (section 5), although the density of instrumentation varies by experiment with some replicating sensors only at the treatment level and others including measurements for each replicate plot. These studies employ different methodologies, including using either natural studies or experimental manipulations and active or passive treatments (Beier et al. 2012; Hanson 2000). For these studies, treatment is defined as the type of manipulation imposed over replicate plots. Experiments also differ in the number of treatment levels used, a design consideration that can critically influence an experiment's usefulness in informing models (Cottingham et al. 2005). Below, we highlight the strengths and weaknesses of different methodologies for improving and informing how LSMs model biological responses to precipitation change.

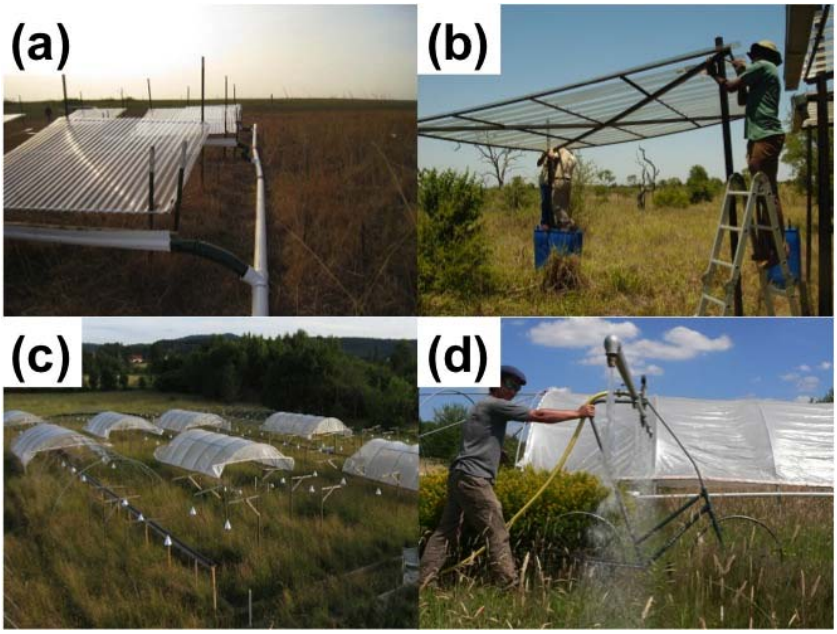

Figure 2 Examples of different experimental designs employed in precipitation manipulation experiments. (a) Rainfall exclusion at Konza prairie in Kansas, USA. Note the use of pipes for funneling runoff away from plots. (b) Set up of rainfall exclusion structures at Kruger Park in South Africa. (c) EVENT rainfall exclusion and warming experiment in Germany. Note the use of "control" structures without rain exclusion plastic. (d) Rainfall addition application at the EVENT experiment in Germany with rainfall exclusion shelter in the background.

Natural Studies Versus Experimental Manipulations

Research designed to study how land surfaces respond to precipitation will usually follow one of two strategies: (1) utilize existing natural precipitation events or gradients within a single ecosystem or (2) manipulate precipitation through the use of experimental treatments. Natural experiments allow for the evaluation of large-scale responses (e.g. full system gas,

energy, and water fluxes). For example, flux tower data at interannual and intraannual scales have been utilized for describing the response of whole-system fluxes to drying and rewetting cycles in Mediterranean regions, finding that these systems are sensitive to spring rain (Aires et al. 2008; Allard et al. 2008; Ma et al. 2007). Other examples include studying the response of systems to anomalous conditions such as extreme droughts (Baldocchi, 1997; Leuzinger et al. 2005; Reichstein et al. 2007) and rain pulses (Huxman et al. 2004a, 2004b; Jarvis et al. 2007; Jenerette et al. 2008; Ma et al. 2012). Also, eddy flux networks have allowed for cross-system comparisons of precipitation responses and changes in water use efficiency (Keenan et al. 2013; Rambal et al. 2003; Ross et al. 2012). These types of studies are useful for examining how processes defined and modeled at smaller scales translate to larger scales (Baldocchi, 1997; Rambal et al. 2003; Vargas et al. 2013), as is described in section 7. Natural experiments are also better for evaluating responses over long time scales, as most precipitation manipulation experiments last 1–3 years and those lasting greater than 10 years are rare (Beier et al. 2012). Although natural studies are well suited for analyzing precipitation responses at large scales, in terms of improving LSMs, they suffer from the fact that the responses observed could be the result of numerous smaller-scale processes, which cannot be easily disentangled. For example, at a single site and/or between sites, seasonal changes in abiotic factors such as temperature or photoperiod or biotic factors such as vegetation species distribution or soil type could influence perceived precipitation responses. Therefore, natural studies are best suited for formulating predictions that can be subsequently tested using more controlled experiments and/or examining the results of small-scale experiments at larger scales (section 7). Here we will primarily focus on smaller-scale manipulation studies but include a discussion on how these and larger-scale data can be used in conjunction to evaluate model performance. As opposed to natural studies, precipitation manipulation experiments evaluate the response of the land surface to changes in precipitation through direct alteration of the amount and/or timing of precipitation (Figure 2). Most often these experiments manipulate rainfall (i.e. warm-season precipitation) rather than full-season precipitation, but for the purpose of this review, we will use the term precipitation. These manipulative experiments will often include control plots to use for comparison to the manipulated, or experimental, plots. These control plots may experience ambient conditions defined by the precipitation pattern at the site or prescribe conditions often representing mean precipitation patterns at the site. Depending on the plot size, a buffer zone and/or trenching will be used to minimize edge effects, separate plots, and improve the treatment representativeness (Hanson 2000).

Active Versus Passive Manipulations

Precipitation manipulation experiments commonly employ either active or passive treatments or both. In active manipulation studies, precipitation is artificially added to plots using sprinklers, hoses, or watering cans to supplement or replace natural precipitation or to alter precipitation chemistry. Alternatively, passive manipulations augment or remove ambient precipitation, typically through rainfall interception using throughfall or overstory shelters (Hanson 2000). In areas where vegetation height is low, such as grasslands, overstory shelters are typically employed (e.g. Hoeppner & Dukes 2012; Koerner & Collins 2014; Yahdjian & Sala 2002), whereas throughfall shelters are typically used in systems with tall vegetation, such as forests (e.g. Borken et al. 2006; Hanson et al. 1998; Pangle et al. 2012) (but see Misson et al. (2010)). Due to logistical issues, these experiments are often done at small (tens of meters) scales (Beier et al. 2012). However, experiments at larger scales have been performed (e.g. Hanson et al. 1998; Misson et al. 2010; Nepstad et al. 2002; Pangle et

al. 2012). The benefit of active manipulations is that environmental conditions other than precipitation are minimally altered as a result of the manipulations. With passive manipulations, researchers must be cautious of unintended changes in radiation, temperature, or vapor pressure deficit that might result from treatment structure.
In cases where these effects may be confounding, control plots are typically adjusted to create similar conditions to the experimental plots (e.g. by using netting to block out radiation similar to that removed by an overstory shelter). Also, the conditions created by passive manipulations are reliant on ambient conditions. Therefore, interannual differences in precipitation responses may be larger than responses to the manipulation due to year-to-year variation in precipitation.

Number of Treatment Levels

A major dilemma in the design of precipitation manipulation experiments involves determining the number of treatment levels and number of replicates of each treatment. As precipitation is an environmental driver that occurs at a range of values, multiple experimental treatment levels are desirable (Cottingham et al. 2005). However, due to logistical constraints, an increase in treatment levels often comes at a cost to replication. Experimental designs that employ only a single treatment level typically have higher replication, often of a precipitation regime expected for a given region (e.g. Jentsch et al. 2007). These analysis of variance-type designs may increase confidence in evaluating the response to a particular scenario but do not allow for responses to be evaluated across a range of precipitation and/or soil moisture values. In most LSMs, the biological responses to changes in precipitation are manifested as a function of rainfall interception and soil moisture/soil water potential levels. Thus, experimental data that can be regressed across multiple treatment levels can be integrated easier into LSMs (Cottingham et al. 2005).

However, because of the trade-off between number of treatments and number of replicates in precipitation manipulation experiments, the uncertainty of a model formulation informed from data generated using multiple treatment levels likely increases as the number, range, or replication of levels decreases. Another source of uncertainty arises when the treatment levels fail to encompass soil moisture levels (and variability) expected under future scenarios. This may be particularly true for heavy rainfall or drought events. In fact, experiments that push the system to or beyond the most extreme multimodel projections for a given area can provide the unique ability to identify thresholds in precipitation that severely limit ecosystem functioning (Smith 2011). Therefore, ideally, experiments should be designed to include multiple treatments leading to a range of soil moisture values that capture and extend beyond the range of past observations and mean projections. Typical output from these experiments includes soil moisture, aboveground net primary productivity, leaf onset and offset dates, soil respiration, and species composition, among others (Table 1). As we discuss in the following sections, with the addition and adjustment of a few measurements or products, the applicability of these measurements to models, and thus progresses in the broader global change community, could be greatly improved.

Table 1 Data needs to incorporate commonly measured field responses into current-generation models

Process	Common responses measured and reported by the experimental community	Data needed by the modeling community[1,2]
All processes	▪ Precipitation amount and timing ▪ Soil moisture ▪ Air temperature	• Soil moisture, preferably at high temporal and spatial resolution (actual and relative to saturation) • Soil water retention curves • Precipitation amount and timing • Energy, water, and carbon fluxes • Micrometeorological data (e.g. air temperature, humidity, radiation, wind speed), preferably at high temporal and spatial resolution • Soil temperature • Detailed site characteristics (e.g. plant functional and soil types and fractions)
Carbon assimilation and productivity	▪ Aboveground net primary productivity ▪ Net photosynthesis	• Photosynthesis and respiration, preferably at high temporal resolution and in multiple canopy layers • Stomatal conductance • Carbon allocation to different plant tissues including changes in carbon stocks over time
Phenology	▪ Date of bud burst/emergence ▪ Leaf drop/senescence	• Estimates of moisture availability and demand at similar time points before, during, and after emergence/senescence • Comparisons across multiple seasons to explore thresholds • LAI, preferably at high temporal and spatial resolution
Soil organic matter decomposition	▪ Soil respiration	• Soil respiration, preferably at high temporal and spatial resolution • Microbial abundances at multiple depths • Litter decomposition rates
Plant community dynamics	▪ Species richness ▪ Species diversity	• Species abundances grouped by functional type • Functional type shifts through time • Rates of reproduction and mortality

[1]Measurements are grouped by order of importance.

5 Data Needs for Integration of Experiments With Models

To integrate experimental responses into LSMs, high-resolution monitoring of environmental variables is needed (Table 1). One obvious response is the change in water flow through the system as a result of precipitation change. In general, precipitation within LSMs can take three possible routes: (1) fall on the vegetation where it is intercepted and subsequently evaporated or fall on the ground as drip, (2) fall on the soil surface where it can infiltrate the soil and then evaporate, be taken up by plant roots, or percolate down to add to deeper layers including groundwater supplies, or (3) run off from the surface (Figure 3).

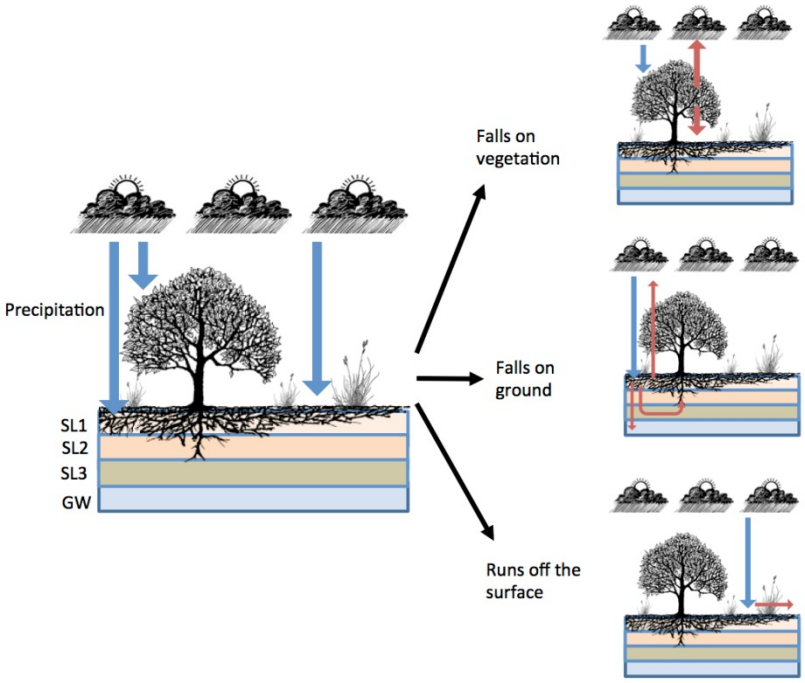

Figure 3 Scheme of the land water balance within a hypothetical LSM with three soil layers. In this example, and similar to the description in the text, precipitation can either (1) fall on the vegetation where it is intercepted and subsequently evaporated or fall on the ground as drip, (2) fall on the soil surface where it can evaporate or infiltrate the soil and be taken up by plant roots or percolate down to add to deeper layers including groundwater supplies, or (3) run off from the surface. SL=soil layer, GW=ground water.

Different routes are a function of vegetation, soil properties, and rainfall intensity. The result is a general water budget relationship between soil water content in depth units (SWC), precipitation (P), evapotranspiration (ET), runoff (R), and addition to groundwater storage (GW): SWC = P-ET-R-GW. In LSMs, water kept in the soil column (i.e. SWC) is generally allowed to flow in the vertical direction (e.g. z component), with the number of soil layers varying between models (e.g. Famiglietti & Wood, 1994; Liang et al. 1994) (but see Seneviratne et al. (2010) for a detailed review). Horizontal flow is typically accounted for only in hydrological and ecohydrological models (e.g. Fatichi et al. 2012b). To compare the hydrological budget of the system with observations, an estimate of these variables (commonly just SWC or ET, along with P) is needed. Soil moisture can be considered a unifying theme for the land surface because it exerts a control on many physical and biological processes (Legates et al. 2011). Multiscale processes, such as leaf gas and water exchange, phenology, and decomposition, respond indirectly to changes in precipitation through direct responses to soil moisture or soil water potential (Cramer et al. 2001), an energetic measure of soil water content (Hillel, 1998). Even though plant and microbial

processes are mostly governed by soil water potentials, soil moisture is the variable commonly monitored (Famiglietti et al. 2008; Jacobs et al. 2004; Robock et al. 2000; Rosenbaum et al. 2012) and needs to be converted in soil water potential levels using soil water retention curves (Saxton & Rawls 2006; van Genuchten, 1980) especially for modeling applications that simulate both soil moisture and water potentials (e.g. Ivanov et al. 2008b; Porporato et al. 2001). Soil moisture can be observed using direct gravimetric sampling or neutron probe measurements but is most commonly monitored using time domain reflectometry (TDR; see Rundel & Jarrell (2000), Hanson (2000), and Robinson et al. (2008) for more detail information about each technique). The benefit of TDR is that it can be implemented in a nondestructive fashion. However, TDR provides an estimate of soil water content, and further data, such as a soil water retention curves and/or soil texture, are needed to translate the data into soil water or matric potential. As such, researchers should be careful about comparing moisture responses between studies reporting only soil water content data, as similar values may imply differing amounts of stress in multiple systems that vary in soil texture (Vicca et al. 2012). There is still uncertainty in how precipitation influences soil moisture both directly and indirectly (e.g. through vegetation-driven changes in soil infiltration, shading, or rain funneling (D'Odorico et al. 2007)), and models are not always able to simulate these responses well. High spatial and temporal resolution monitoring within precipitation manipulation experiments could help reduce model uncertainty. In the field, soil moisture measurements often have better temporal, rather than spatial, resolution, particularly with depth (Robinson et al. 2008; Vereecken et al. 2008). As more models are beginning to include multiple soil layers (e.g. Amenu & Kumar 2008; Drewry et al. 2010; Oleson et al. 2013; Parton et al. 1993) and topographic heterogeneity (Fatichi et al. 2012a; Ivanov et al. 2008a), soil moisture measurements at a variety of depths and locations are important, as soil moisture can vary within the vertical profile and among sites with similar soil characteristics (e.g. He et al. 2013). More general, in models soil moisture is a function of climate, but this is mediated by the characteristics of the site, including plant functional types (PFTs), soil type and texture, and rooting density and depth. Therefore, monitoring and reporting of general site characteristics along with moisture values are necessary for proper model parameterization (Ivanov et al. 2012; Liang et al. 2005) and/or data assimilation products (Heathman et al. 2003; Rodell et al. 2004). In addition, site characteristic monitoring may allow for the inclusion of dynamic responses (i.e. characteristics that change over time) of these variables (e.g. rooting profiles) into models. Note that all aspects of the precipitation-soil moisture interaction cannot be evaluated within experiments, cloud-soil moisture feedbacks in particular. Previous studies have found a strong coupling between precipitation and soil moisture that suggests that soil moisture may feedback to observed precipitation patterns (D'Odorico & Porporato 2004; D'Odorico et al. 2007; Koster et al. 2009, 2004; Teuling et al. 2006). While these dynamics can be accounted for in coupled land surface climate models, they cannot be addressed by small-scale experiments and remain a pure modeling domain. Because the biological processes within LSMs respond to soil moisture/soil water potential rather than precipitation, some have called for precipitation manipulation experiments to begin using common metrics for evaluating soil moisture stress (Vicca et al. 2012). This is important for comparing the results of multiple studies and may also be useful for making generalizations for models. Typically, this requires site characteristic data that can be used to calculate a common metric from measured data (e.g. extractable water or stress intensity; see equations in Vicca et al. (2012)). These data can then be used to generate generalized functions that combine both plant physiological and soil processes to describe the response of plant water uptake to soil moisture (e.g.

Bartholomeus et al. 2008; Caylor et al. 2009; Ivanov et al. 2008b; Porporato et al. 2001). These functions, essentially plant responses at different levels of soil water potentials (e.g. Feddes et al. 1976, 2001; Maherali et al. 2004, 2006), allow models to accommodate combinations of plant and soil types with differing responses. Finally, micrometeorological data such as soil and air temperatures at various depths and heights, respectively, as well as solar radiation, wind speed, and humidity at different points within the canopy are useful for improving and testing model functioning (Katul et al. 2012; LeMone et al. 2007; Seneviratne et al. 2010). These data can be used to facilitate the incorporation and test the usefulness of more refined processes into models (i.e. processes that respond only in part to changes in moisture), such as those detailed in the next section. See Table 1 for a description of general data necessary to incorporate processes into a model as well as specific data necessary to incorporate the four processes discussed below.

6 Experimental Data Best Suited for Integration With Models

In the following subsections we compare four biological processes commonly measured in the field with their model analogs: (i) carbon assimilation and productivity, (ii) phenology, (iii) soil organic matter decomposition, and (iv) plant community dynamics. We chose these processes because they range in scale from leaf to ecosystem level and are affected by precipitation over differing time scales ranging from seconds to decades (see Figure 1). This range allows us to discuss differences in measured and modeled processes over differing spatial and temporal scales. The purpose of these comparisons is to highlight examples of processes that are measured differently than they are modeled and to explore how measurements or formulations could be designed differently to help make experimental results more suitable for model development. Many of the recommendations provided could be applied to other processes beyond those mentioned below.

Carbon Assimilation and Productivity

Within LSMs, net primary productivity is the difference between simulated carbon assimilation and autotrophic respiration. Carbon assimilation is simulated through leaf gas exchange processes that respond to changes in environmental conditions, including soil moisture. However, the structure of these soil moisture responses varies greatly among models (De Kauwe et al. 2013; Egea et al. 2011a). Some models (e.g. Orchidee-CN (O-CN) (Zaehle et al. 2010)) use a modifier to alter the relationship between photosynthesis and conductance within coupled photosynthesis-stomatal conductance schemes, which are based on empirical relationships between stomatal conductance and assimilation (e.g. Ball et al. 1987; Jacobs et al. 1996; Leuning, 1995). These modifiers are based on soil water content (e.g. Fatichi et al. 2012b; Wang & Leuning, 1998), soil water potential (e.g. Laurent 2004), or leaf water potential (e.g. Vico & Porporato 2008). See Figure 4 for an example of such a function. Alternatively, other models (e.g. Community Land Model (CLM) (Oleson et al. 2010, 2013)) include a similar type of modifier that alters the biochemical capacity of the photosynthetic system based upon the soil water available to plant roots. For example, CLM uses a scaling factor, βt, which scales down the maximum rate of carboxylation of photosynthesis (Vcmax). The βt value ranges from 0 to 1 depending on the amount of roots and soil moisture in each soil layer (i.e. Vcmax will be decreased less if a greater amount of water is available to a larger fraction of roots). This modified Vcmax value is then used to calculate photosynthetic rates (Collatz et al. 1991; Farquhar et al. 1980). The carbon that is

taken up through photosynthesis is then allocated to different processes, including growth (Oleson et al. 2013). As opposed to models that simulate photosynthetic responses to moisture and infer productivity responses, field experiments often directly measure productivity and infer that photosynthesis is a main factor driving the response (e.g. Fay et al. 2003). This is because the positive relationship between precipitation, moisture, and aboveground production is well documented and the explanation for this pattern is well understood: when soil water is abundant, a plant can leave its stomates open, allowing for greater CO_2 diffusion into leaves (Chaves et al. 2009, 2003, 2002; Niyogi & Xue 2006; Pinheiro & Chaves 2011; Potter et al. 1993; Shaw et al. 2002).

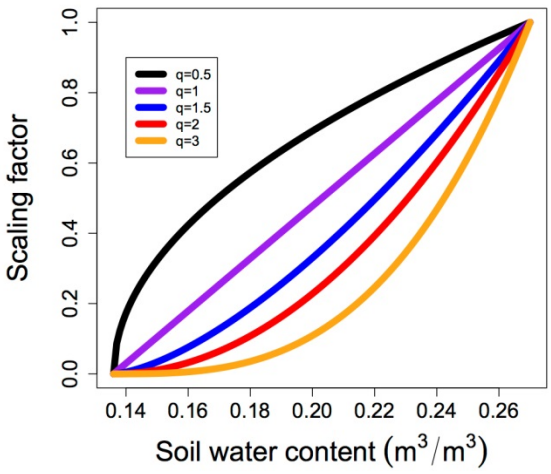

Figure 4 Conceptual example showing values of a typical soil moisture scaling factor for a land surface process (e.g. photosynthesis, SOM decomposition, etc.) under different soil moisture conditions (θ). The process modeled here is for photosynthesis, but a similar theory applies for other processes. The function plotted defines the scaling factor to be 1 above a critical value when moisture does not influence the process (θ_c; 0.27 m^3/m^3 here), 0 below the permanent wilting point (θ_w; 0.136 m^3/m^3 here), and $((\theta - \theta_w)/(\theta_c - \theta_w))^q$ elsewhere, where q is a measure on non-linearity that describes the shape of the function (Egea et al. 2011a; Keenan et al. 2010; Porporato et al. 2001). Data are plotted for q values of 0.5, 1, 1.5, 2, and 3.

However, other evidence suggests that the link between assimilation and growth is more complex because of the lag between assimilation and allocation of carbon (Sala et al. 2012). This link may indeed be mediated by plant carbon storage and hydraulic controls acting directly on meristematic activity (tissue growth) rather than photosynthesis (Fatichi et al. 2014; Körner 2013). In addition, in hydric sites, water is not limiting and additional water can decrease soil oxygen concentrations and nutrient cycling, resulting in nutrient leaching and decreased aboveground productivity (Schuur 2003). Unfortunately, many studies do not fully link the flow of carbon (from photosynthesis to growth), limiting their ability to develop model parameterizations because models rely on a structure that links changes in growth in response to moisture availability through carbon uptake and allocation. As such, there remains a need to better elucidate these responses in the field (Table 1). An additional area of uncertainty in the field and in models is the interactive effect of elevated CO_2 and water stress on carbon assimilation and productivity. Water use efficiency (i.e. the amount of carbon gained through assimilation per water lost through transpiration) has been shown to increase with experimental and historical increases in CO_2 (Battipaglia et al. 2013; Keenan et al. 2013; Morgan et al. 2011), but the ability of these potential water savings to mitigate drought stress, increase runoff, and stimulate productivity remains debated (Donohue et al. 2013; Fatichi & Leuzinger 2013; Huntington 2008; Warren et al. 2011; Zaehle et al. 2014). Direct experimental tests of this response on plant productivity are rare and suggest little interactive effect (Dukes et al. 2005). Observational studies suggest that enhanced water use efficiency does not always translate into productivity gains (Peñuelas et al. 2011) or mitigate the impacts of soil moisture stress on plant growth (Brzostek et al. 2014; Grünzweig & Körner

2001; Morgan et al. 2004). As models vary greatly in how they simulate photosynthesis and conductance responses to CO_2 and soil moisture (De Kauwe et al. 2013), there is the potential for an important synergy between field researchers and modelers to address this knowledge gap. Currently, model simulations of terrestrial productivity responses to changes in precipitation are challenging, likely due to improper parameterization of photosynthetic responses and/or the connection between assimilation and productivity (Powell et al. 2013). In fact, model-data comparisons have found that models that only include Vcmax responses to soil moisture are not able to reproduce observations as well as models that include more physiologically relevant mechanisms (Egea et al. 2011a) (but see Keenan et al. (2010)). As such, there has been a recent push to include more physiologically relevant responses into models (e.g. mesophyll conductance (Egea et al. 2011a)). Although these studies are a good start, systematic model-data comparisons examining photosynthetic and/or growth responses to changes in soil water content are lacking. Although poor parameterization of stomatal conductance, assimilation, and growth responses to soil moisture is a major limitation of current models, this limitation provides an opportunity for future field experiments to help understand and quantify these responses. To help improve model performance, field researchers should measure the photosynthetic and conductance responses (e.g. Egea et al. 2011b; Grassi & Magnani 2005; Rodgers et al. 2012) and link them to the allocation processes that lead to changes in growth (Franklin et al. 2012). Figure 5 illustrates how in the absence of this link, field-derived productivity data, while useful for evaluating the overall model performance, may not aid in improving the parameterization of underlying processes. It also is worth noting that model simulation of these responses is difficult because of the need for current models to organize species into broad categories, or plant functional types (PFTs), and to be able to account for microclimate (e.g. temperature, radiation, humidity, and wind speed) variability within the plant canopy.

Phenology

Shifts in phenology can have important feedbacks on ecosystem processes, particularly carbon uptake, biotic interactions, and energy-water linkages (Dragoni et al. 2011; Richardson et al. 2009, 2012). Phenological responses to soil moisture in LSMs are often only simulated in “raingreen” deciduous species (i.e. species that shed their leaves in response to soil moisture stress). This is implemented by simulating leaf senescence in these trees as a function of the ratio of soil moisture and canopy conductance (e.g. Sitch et al. 2003). Phenology in other deciduous plant functional types (i.e. “summergreen” species) responds to temperature rather than soil moisture. In some models, phenology in deciduous species may be determined by either temperature, day length, or moisture depending on which factor reaches a predetermined threshold first (e.g. Fatichi et al. 2012b; Shevliakova et al. 2009). Similar alternative models have also been proposed to determine phenology in deciduous species based on a cost-benefit structure, where leaves are only present when environmental conditions, including temperature, precipitation, and photoperiod (an important driving factor (Körner & Basler 2010)), result in a net carbon gain (e.g. Arora & Boer 2005). Unfortunately, manipulation experiments in areas where phenology is most likely driven by soil moisture (e.g. monsoon regions and tropical dry forests (Eamus, 1999; van Schaik et al. 1993)) are scarce (but see Borchert (1994)). As such, it remains unclear how to properly parameterize phenological responses in these biomes. Phenological studies examining precipitation responses in temperate systems typically find that temperature drives phenology (Bloor et al. 2010; Cleland et al. 2006). However, flux tower studies in Mediterranean grassland (Xu & Baldocchi 2004; Xu et al. 2004) and precipitation

manipulation experiments in temperate grassland (Jentsch et al. 2009), Mediterranean shrubland (Llorens & Peñuelas 2005), and Mediterranean forest (Misson et al. 2011) have shown that moisture can have a strong effect on phonological responses in extratropical systems, typically delaying spring phenology under drier conditions. For example, Misson et al. (2011) found that the number of Mediterranean trees producing functionally mature leaves was decreased by 50% under heavy (87% removal) spring drought.

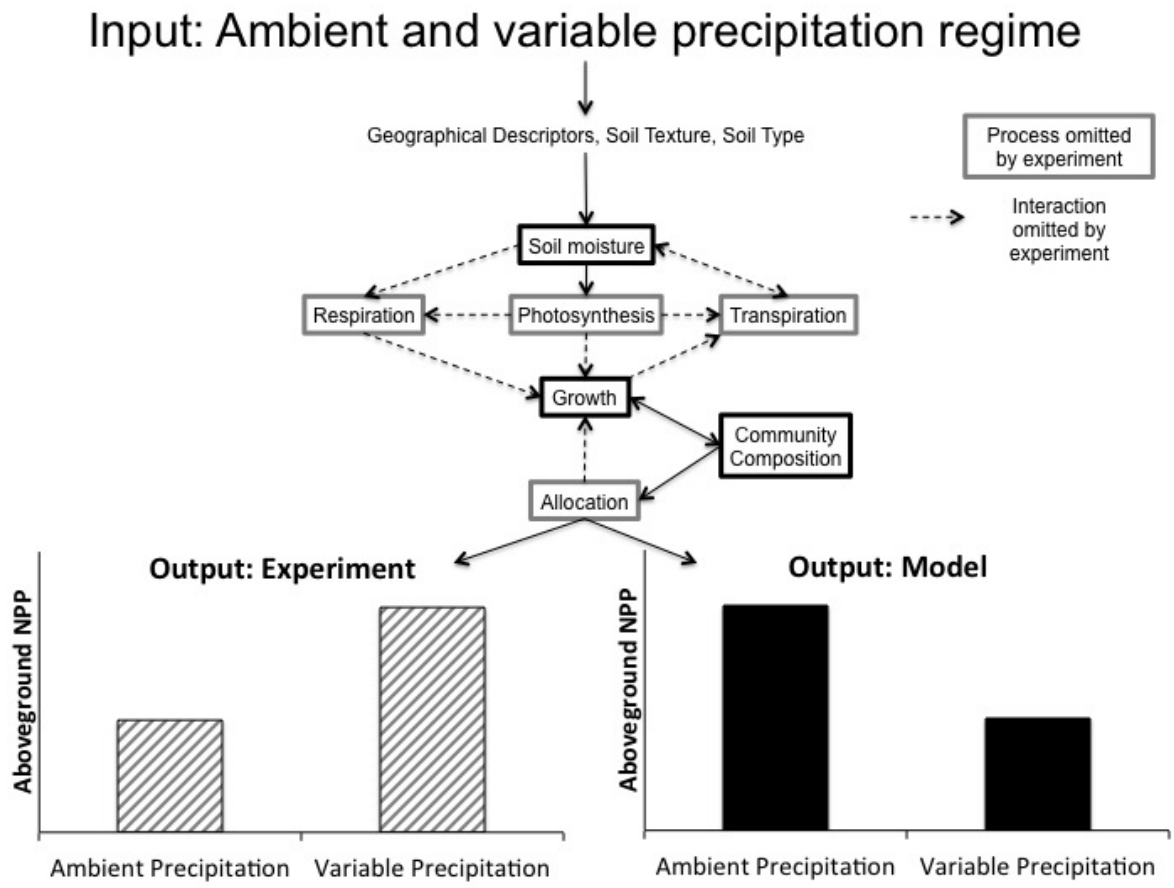

Figure 5 Conceptual diagram illustrating the potential disconnect between models and experiments. Both experimental (left side) and modeling (right side) studies use the same inputs (i.e. ambient and variable precipitation) and generate the same output (i.e. aboveground net primary production (ANPP)). Boxes and arrows show each modeled process and interaction, respectively. However, grey boxes and dashed arrows show processes and subsequent interactions, respectively, not examined in the experimental study. As an example, the two studies result in different conclusions as to how a more variable precipitation pattern would affect ANPP. However, these cannot be reconciled due to the fact that the two studies do not measure (experiment) or simulate (model) the same processes. Therefore, although these experimental data would show that the model does not correctly represent the treatment response, it would be difficult to reformulate the modeled processes using this experiment.

Better model representation of phenological responses to precipitation change is likely to have a large influence on model performance. Similar to productivity, field experiments should not only measure typical changes in phenology such as timing of bud burst and leaf drop but also carefully measure how these processes vary with changes in moisture availability and demand across seasons as well as within seasons (e.g. time evolution of leaf area index (LAI) at high temporal resolution), carefully noting threshold moisture values

where phonological shifts occur. Studies should consider overstory as well as understory phenology, as understory plants have been shown to constitute a large portion of carbon flux in some ecosystems (Baldocchi et al. 1997), an effect that, due to the phenology of these species, has been shown to impair model performance (Kimball et al. 1997). These types of measurements will allow for a much better incorporation of responses and processes into LSMs.

Soil Organic Matter Decomposition

It is well known that soil organic matter (SOM) decomposition is sensitive to changes in water availability (Ise & Moorcroft 2006; Manzoni & Porporato 2009; Moyano et al. 2013; Schimel et al. 1994; Suseela et al. 2012).Many LSMs simulate SOMdecomposition in a similar fashion (Todd-Brown et al. 2013), using a framework similar to the CENTURY model framework (Parton et al. 1987, 1993). In the CENTURY framework, decomposition is modeled as a first-order kinetic reaction with rate constants that differ as a function of the reactivity of carbon in various soil and litter pools (i.e. passive, slow active (Parton et al. 1987, 1993)). To model climate responses for each pool, this rate constant is modified as a function of soil temperature following Arrhenius kinetics (Lloyd & Taylor, 1994). Soil moisture influences this response by altering soil temperature. Soil moisture is also included as a direct influence along with the temperature function into these models in the form of an increasing (e.g. Andrén & Paustian, 1987) or peaked (e.g. Coleman & Jenkinson, 1999) modifier, similar to the Vcmax scalar, βt, noted above. In the field, SOM decomposition responses to precipitation and moisture are well studied. It is understood that when soil moisture is low, soil microbes become less active, exhibit stress responses, and have less access to C- and N-bearing substrates (Schimel et al. 2007). When soils are water saturated, anoxic conditions can impede microbial and enzymatic activity (Freeman et al. 2001). Thus, shifts in precipitation that lead to dry or wet conditions appear to lead to strong declines in decomposition rates (Liu et al. 2009; Suseela et al. 2012) and these responses are typically included into models (e.g. Porporato et al. 2003). On the other hand, shifts in precipitation that move soil moisture conditions away from these wet and dry thresholds into more optimal conditions stimulate decomposition often leading to large pulsed releases of carbon and nutrients (Cleveland et al. 2010; Craine & Gelderman 2011). For example, in arid and semiarid ecosystems, rainfall events that follow long periods of dry conditions lead to pulsed releases of CO_2 and nutrients (Carbone et al. 2011; Huxman et al. 2004a; Sponseller 2007; Xu et al. 2004). These pulses in soil respiration and N mineralization can comprise a substantial portion of the annual production of CO_2 and plant-available N (Austin et al. 2004; Carbone et al. 2011). Models could be tested to reproduce pulse respiration events and nonlinear threshold responses (Todd-Brown et al. 2013), but further evaluation of model performance is necessary, as these responses may become less apparent and less important when evaluating carbon cycling over longer time scales. This is only possible with longer manipulation experiments or larger-scale observations (section 7). In addition, different types of soil organisms have different strategies for acquiring and utilizing soil carbon and nutrients, an effect that may have a large influence on soil carbon stocks (Averill et al. 2014; Orwin et al. 2011). These organismal differences are basically unaccounted for in LSMs (Manzoni & Porporato 2009). Recent research has focused on explicitly representing soil microbial processes into ecosystem models (Allison et al. 2010; Orwin et al. 2011; Treseder et al. 2012). At the global scale, the integration of a functioning soil microbial community into CLM substantially improved predictions of current soil C stocks (Wieder et al. 2013). The majority of the parameters and outputs of this CLM microbial model can be

measured in the field (i.e. microbial growth efficiency, microbial biomass, and enzyme activity) and should be more often reported as experimental results. Given that enzyme kinetics and microbial growth efficiency are modeled primarily as a function of soil temperature in most microbial models, there is the potential for field researchers to directly inform the next generation of models by investigating how these parameters vary as a function of experimental changes in soil moisture or, better, soil water potential (via changes in precipitation).

Plant Community Dynamics

A few models have been designed to incorporate individual- and community-level processes such as survival and competition into ESMs through the use of dynamic global vegetation models (DGVMs). However, DGVMs typically have a simplified land surface component, and integration of state-of-the-art LSMs with ecosystem demography dynamics for global-scale analyses is still limited (e.g. Arora et al. 2013). DGVMs typically come in three classes: (1) "area-based" models that simulate the plant functional type (PFT) occupancy of a grid cell based on environmental and climatic variables in a deterministic manner (e.g. CLM (Bonan et al. 2002; Oleson et al. 2010, 2013), Lund-Potsdam-Jena (LPJ) (Sitch et al. 2003), and Top-down Representation of Interactive Foliage and Flora Including Dynamics (TRIFFID) (Cox 2001)), (2) "individual-based" gap models that simulate competition between individual plants, primarily for light, in a stochastic manner (e.g. LPJ General Ecosystem Simulator (Smith et al. 2001) and the adaptive dynamic global vegetation model (Scheiter & Higgins 2009)), and (3) hybrid models that simulate succession and light competition between PFTs in a deterministic, computationally efficient manner (e.g. EcosystemDynamics Model (Medvigy et al. 2009; Moorcroft et al. 2001)). Individual responses in individual-based and hybrid DGVMs are typically defined primarily by light competition, while changes in soil moisture affect vegetation at the community level. Community responses are primarily driven by feedbacks that differ between PFTs (e.g. Medvigy et al. 2009). In essence, these responses are similar to the ones presented above but are parameterized differently for different PFTs or species. For example, models may employ lower moisture stress thresholds for drought-tolerant than drought-intolerant species, which have higher water use efficiency. This allows community dynamics to play out via differences in carbon uptake of different PFTs under different moisture conditions. Additionally, ESMs may simulate plant community changes to precipitation indirectly through changes in fire occurrence (Li et al. 2013). However, as human disturbances/decisions are critical in driving fire projections, we focus on more direct precipitation responses here. Although DGVMs are typically combined with LSMs to simulate plant community responses, experimental results suggest that precipitation responses of plant communities are more complex than those represented in models (e.g. Balvanera et al. 2006; Barger et al. 2011; Knapp, 1993; Knapp et al. 2012; Pérez-Ramos et al. 2010; Walter et al. 2012; Yachi & Loreau, 1999). For example, increases in rainfall intensity may specifically alter the distribution of PFTs by increasing shrub encroachment (Barger et al. 2011; Kulmatiski & Beard 2013), which could, in turn, influence the microclimate of the system (He et al. 2011). Changes in rainfall amount may affect seed production (Pérez-Ramos et al. 2010), and changes in rainfall timing may also affect seed germination (Chou et al. 2008; Rivas-Arancibia et al. 2006), an important effect in annual species. Finally, evidence suggests that biodiversity increases functional resilience to environmental fluctuations (Balvanera et al. 2006; Yachi & Loreau, 1999), with other experimental evidence suggesting that more functionally diverse communities experience less tissue dieback under extreme drought (Walter et al. 2012). These community responses

can potentially be included into models using a PFT approach (e.g. by allowing for shifts in PFT composition under different soil moisture levels or stresses); however, experimental data are still insufficient for providing thresholds necessary for parameterization of these responses in different biomes and likely a very large within biome variability has to be expected. More data on reproduction and mortality of different species are anyhow warranted. More likely these responses could be incorporated using a trait-, rather than PFT-, based framework for modeling species heterogeneity. A trait-based framework involves employing known relationships between plant traits that arise a consequence of evolutionary tradeoffs (Osnas et al. 2013; Reich 2014; Wright et al. 2004) to describe species distributions in time and space (Van Bodegom et al. 2012). This work is promising in that it overcomes many of the problems associated with using PFTs (e.g. few PFT levels and many individual parameterizations); however, this work is still in its infancy (Douma et al. 2012; Pavlick et al. 2013; Scheiter et al. 2013).

Scales of Responses

Long-term (>10 years) precipitation manipulation experiments are rare (Beier et al. 2012). Short-term experiments may be able to adequately explore the response of stomatal functioning or fortuitously capture extremes. However, responses such as plant and/or microbial species change may not be able to be observed over the short time scales utilized in most experiments (Figure 1) (Smith et al. 2009). This is also important for model development, as the processes that respond to longer-term changes are typically higher-level processes (e.g. phenology on the scale of a season and plant community dynamics on the scale of years to decades). These higher-level processes ultimately define lower level processes and, thus, can be critical for model functioning. For instance, it is rather different for a model to reproduce the plant response to a few days-long drought or to several years of below average precipitation. To highlight the importance of this issue, we developed a simple model sensitivity experiment. We evaluated model sensitivity of the carbon assimilation, SOM decomposition, phenology, and community composition processes above using the land component of the NOAA/GFDL ESM (LM3) (Shevliakova et al. 2009). We ran simulations at a grid cell corresponding to a temperate deciduous broadleaf forest flux tower site in Indiana, USA (Dragoni et al. 2011), for 7 years (1999–2005) following a 299 year spin-up. The model structures used included a base version of the model (Shevliakova et al. 2009), as well as versions that (1) increased conductance limitation under drought stress by a factor of 2 (carbon assimilation), (2) increased the moisture level at which leaves drop by a factor of 1.5 (phenology), (3) changed the SOM decomposition-soil moisture function from a peaked to constantly increasing function (SOM decomposition), and (4) altered the PFT distribution from 100% temperate deciduous trees to a 50–50 mix of temperate deciduous trees and C3 grasses (community responses). See the supporting information for a full description of the sensitivity study. Our results confirmed the idea that models are most sensitive to higher level processes, particularly shifts in vegetation cover, as changes to the PFT distribution had the largest effect on the modeled NEE, increasing NEE by 36%, compared to a <5% change for alterations to leaf gas exchange, phenology, or SOM decomposition functions (Figure 6). This may be surprising considering that leaf gas exchange, phenology, and SOM decomposition are more closely linked to the carbon flux of the system (i.e. NEE). However, within the model, changes in PFT structure outweigh relatively subtle changes in leaf gas exchange and SOM decomposition. PFT structure ultimately describes the magnitude of change that occurs as a result of changes in these lower level processes (e.g. the way in which CO_2 is taken up is determined by the growth and

survival strategy and photosynthetic pathway of the plants within each PFT). While the case study shown here is only for one model formulation under a subjectively chosen set of scenarios, it highlights the critical need for studies to improve the formulations and/or parameterizations for higher-level functions. It is also supported by a recent study which showed that sensitivity of ET and vegetation productivity to changes in annual precipitation increases when an ecosystem undergoes reorganization (e.g. successional and invasion processes, shifts in composition (Fatichi & Ivanov 2014)). In addition, these results highlight the importance of site-level conditions in modeling studies. As such, it is critical that experiments report site conditions such as species distribution and soil type and texture in order to help integrate results with models.

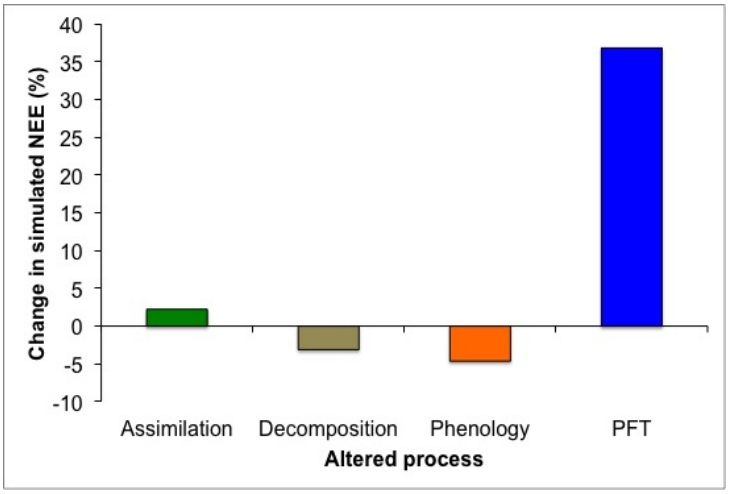

Figure 6 Percent change in simulated net ecosystem exchange (NEE) at the Morgan Monroe State Forest flux tower site from 1999-2005 as a result of an alteration to one of the four processes mentioned in the text compared to a base version of the model (Shevliakova et al. 2009): (1) water stress function on stomatal conductance (g_s) increased by a factor of 2 (green), (2) increasing rather than peaked function for SOM decomposition responses to soil moisture (as in the base model; brown), (3) drought-induced threshold for leaf drop increased by a factor of 1.5 (green), and (4) base model with 50-50 C_3 grass-temperate deciduous tree distribution rather than 100% temperate deciduous trees (as in the base model; blue). See text and supporting materials for simulation details.

7 Connecting Plot-Scale Data With Models Using Intermediate-Scale Observations

Above, we have outlined examples of ways in which plot-scale precipitation manipulation experiments can help to improve LSMs. However, each example often assumes that plot-scale responses will be representative of larger spatial scales (e.g. ecosystem, regional, or global scale). Also, many processes are measured in the field at different temporal scales than their model analogs. For example, leaf gas exchange responses occurring over short time periods (e.g. seconds) in the field must be assumed to be similar when incorporated into or tested against a model utilizing a larger time step. Also, there may be small-scale (i.e. subgrid from a model perspective) variability that can influence the data (e.g. soil moisture differences due to topographic effects or heterogeneity in soils). These spatial and temporal mismatches are likely to invalidate direct comparisons between large-scale models and data from precipitation manipulation experiments. Therefore, ad hoc solutions are often used for making these comparisons (LeMone et al. 2008). One possible solution is to use and develop independent, intermediate-scale data (i.e. data at a scale between the plot level and

the level that the model is functioning) to test models and formulations designed using data from precipitation manipulation experiments, similar to model benchmarking techniques that have been previously proposed (Henderson-Sellers et al. 1993; Luo et al. 2012; Randerson et al. 2009) and carried out (e.g. Egea et al. 2011a; Keenan et al. 2010; Kleidon & Heimann, 1998; Powell et al. 2013; Richardson et al. 2012; Schaefer et al. 2012; Todd-Brown et al. 2013; Vargas et al. 2013). One such effort, the Project for Intercomparison of Land-surface Parameterization Schemes (PILPS) (Henderson-Sellers et al. 1993, 1995), was designed to improve LSMs through comparison and evaluation of different models. This led to a broader understanding of the processes that result in differences between models. For instance, the PILPS project found that soil moisture estimation contributed greatly to differences between models (Henderson- Sellers et al. 1995). Model intercomparisons help to determine the formulation differences between models that lead to uncertainty but do not necessarily pinpoint the particular process or parameterization that needs to be better represented, as indirect and multiple effects may influence these differences. In fact, problems with model functioning may balance out under typical conditions and not manifest until extreme conditions are seen (Niyogi et al. 1999), conditions that may not occur until long into the future. As a solution, parameterization-level (i.e. equation), rather than model-level, studies could be performed to test the influence of the addition and/or change of a particular parameterization within a single LSM, comparing versions of a single model with differing structures in an ensemble mode. For example, one could run two simulations with inputs and forcings from an observational site (e.g. flux tower site). One simulation would use the original formulation or parameterization of a process, while the other would use a formulation or parameterization from a precipitation manipulation experiment. Following the simulations, comparisons to observational data could then be made (e.g. using Taylor scores (Taylor 2001)) to see if the new model outperformed the old model. This would provide an appropriate test for the scalability of the new formulations or parameterizations. Comparisons of model output could be made with any number of available observational data, including flux tower, forest inventory, remote sensing, or aircraft data. In fact, flux tower data sets have been designed, in part, for such studies (Reichstein et al. 2005). Each data source would come with its own set of positive and negative aspects relating to data availability and global coverage, size of the data footprint, and degree to which the data are truly observational, which reflects the amount of post processing needed and assumptions met to obtain usable data. Therefore, careful consideration should be made when choosing the type of data to compare with and, in most cases, it is best to make comparisons to multiple data sets. In addition, the initial conditions and equilibrium spun-up conditions likely play a large influence on model data comparisons at the scale of observations. Therefore, initial conditions, including plant species and SOM quality and amount, among others, should be set to best match the observational site and ensemble simulations should be done to explore the uncertainty related to initial conditions that are unrelated to the model formulation. Following single-model analysis, similar analyses using other models could be performed to test the generality of the response across models. This could be done using a framework similar to that used in PILPS (Henderson-Sellers et al. 1993, 1995). Data from precipitation manipulation experiments could also be used for model-data comparisons, assuming that data used for comparison are independent of data used for model parameterization. Comparisons with data from manipulation studies have been performed for CO_2 enrichment studies (De Kauwe et al. 2013; Fatichi & Leuzinger 2013; Hickler et al. 2008; Warren et al. 2011; Zaehle et al. 2014) but are rare for precipitation manipulation studies (but see Fisher et

al. (2007) and Powell et al. (2013)). The recommendations provided here would help these comparisons to be made more broadly.

8 Conclusions

Current-generation LSMs are becoming more sophisticated, but, as we have shown above, opportunities exist to improve their ability to simulate biological responses to precipitation and soil moisture. Precipitation manipulation experiments provide an excellent structure by which modeled processes can be examined. These field experiments have proved valuable for understanding processes under different hydrological conditions. We propose that if these experiments are conducted with models in mind (Table 1), they can help to improve model realism. This is particularly true if adequate covariates that allow the response of biological processes to be modeled are examined (Figure 5). At least two types of field to model studies could be realized: one using field data to improve mechanistic understanding and reformulate or reparameterize a modeled process, the other testing models using field data as a reference. Similarly, modeling studies are needed that keep experiments in mind, as they can be helpful for defining the processes and parameters that can be directly improved using field measurements (Figure 6). The objective of this review is not to suggest the restructuring of all precipitation manipulation experiments but to highlight the potential value of these experiments to models and to reignite the dialog necessary to reconnect the experiments to models and thus scale findings from the plot to the globe. To summarize, the following are six specific comments and recommendations for helping to improve the connectivity between precipitation manipulation experiments and LSMs:

1. Experimentalists should consider using an experimental design that could help improve models and expand the level of inference of their research by becoming familiar with a model structure and tailoring their experimental design appropriately. This includes using designs with multiple (i.e. ≥ 2) treatment levels to allow for responses to be regressed across a broad range of precipitation and/or moisture values. The targeted model in this case does not matter, as other models will likely be flexible enough to adjust. If the goal of a particular project is to understand how an ecosystem may respond in the future, the connection with modeling studies is particularly necessary.
2. Modelers should encourage this investment by experimentalists and become involved in experimental design, indicating necessary and important measurements. However, modelers should be mindful of experimental limitations and come up with creative ways to incorporate experimental results and validate those results (e.g. using larger-scale observations).
3. Although precipitation manipulation experiments are becoming more common, the responses of different processes across a high spatial resolution are still unknown due to the poor experimental representation of many biomes. As such, experiments in unrepresented biomes, particularly those occurring at high and low latitudes as well as urban biomes, should be prioritized. Input from the modeling community regarding regions that show the highest uncertainty will be of value.
4. Following from 3, many of the responses discussed above occur over long time scales (Figure 1). Therefore, experiments that run over long time periods (>10 years) or capture extremes are particularly valuable.

5. Decreased model performance or increased model uncertainty resulting from the inclusion and/or reparameterization of processes evaluated in the field should not deter modeling studies from examining, and even including, more mechanistic formulations. Getting the right causality for a given mechanism is important, even at the cost of getting a worse model fit, initially. Representing observed processes increases model realism, which results in a decrease in uncertainty in a future, changing world.
6. Following from 5, there is still a need to improve the way in which models are evaluated. For example, contemporary assessments (such as those mentioned previously) may find that a version of a model that omits certain mechanisms performs better than a more realistic version. The conclusion may be made that the more realistic version is worse, when instead more studies are needed to improve its formulation and/or parameterization. In addition, parameterization evaluations are needed to compliment full model evaluations that have been performed or are currently underway.

Precipitation manipulation experiments are an invaluable tool for helping to improve models, and through increased discussion between the different communities, heeding to the recommendations above, greater progress could be made in understanding how terrestrial ecosystems will respond to future change, under hydrological extremes.

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Supporting Information (Manuscript 6)

The supporting information contains the technical details of the model sensitivity study performed in the manuscript along with a list of references cited within the technical details.

LM3 sensitivity simulations

To examine model sensitivity of different biological processes that act at different scales, five simulations using the terrestrial component of the NOAA/GFDL Earth System Model [LM3; Shevliakova et al., 2009]. Each simulation was run at a single 1° grid cell encompassing a temperate deciduous broadleaf forest flux tower site in Indiana, USA [39°N, 86°W; Dragoni et al., 2011]. The model was run for 59 years (1948-2006) following a 247-year spin up (1701-1947), using three-hourly meteorological forcing based on reanalysis and corrected with observations [Sheffield et al., 2006]. The spin up used the first 30 years (1948-1978) of the reanalysis data continuously looped for forcing. Data was analyzed over the years 1999-2005, which corresponded to years where observational at the site was available. Data was matched against observational data to ensure reasonable forcing. The site was chosen, in part, so that initial conditions, namely the plant functional type, could be set up appropriately.

The model structures used included a base version of LM3 [Shevliakova et al., 2009], as well as versions that: (1) increased conductance limitation under drought stress by a factor of two (carbon assimilation), (2) increased the soil moisture level at which leaves drop by a factor of 1.5 (phenology), (3) changed the SOM decomposition-soil moisture function from a peaked to constantly increasing function (SOM decomposition), and (4) altered the PFT distribution from 100% temperate deciduous trees to a 50-50 mix of temperate deciduous trees and C3 grasses (community responses).

In LM3, stomatal conductance is decreased under water stress. This decrease is defined by the ratio of water available to the leaf to water demanded by transpiration, which is defined as stomatal conductance multiplied by the humidity deficit at the leaf surface. This factor is included in conductance calculations when water demand exceeded water available (i.e., the ratio never exceeds 1). In experimental simulation 1, we multiplied this factor by 2 at each time step.

Leaves drop in LM3 when the ratio of average soil water content to saturated soil water content (θ) drops below 0.1. In experimental simulation 2 we increased this critical value to 0.25.

The SOM decomposition response to soil moisture in LM3 is implemented using a scaling factor that ranges from 0 to 1. If θ is equal to or below 0.3, the scalar is set to 0.2. If θ is between 0.3 and 0.6, the scalar is set to equal $0.2+0.8*(\theta-0.3)/0.3$. If θ is above 0.6, the scalar is set to equal $\exp(2.3*(0.6- \theta))$. In experimental simulation 3, we set the scalar equal to $0.2+0.8*(\theta-0.3)/0.3$ at all θ values above 0.3 (i.e., we removed the decrease under high soil moisture).

For experimental simulation 4, we simply changed the PFT structure of the gridcell from 100% temperate deciduous forest to 50% temperate deciduous forest and 50% C3 grassland. This altered a variety of biophysical and biogeochemical parameters including photosynthetic capacity and surface height and roughness.

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8 List of further publications

The following is a list of additional publications, to which I contributed during my work on this thesis:

Urbina, I; Sardans, J; Beierkuhnlein, C; Jentsch, A; Backhaus, S; **Grant, K**; Kreyling, J; Penuelas, J (2015) Shifts in the elemental composition of plants during a very severe drought, *Environmental and Experimental Botany*, **111**, 63-73

Grant, K; Hein, R; Gellesch, E; Nagy, L; Schlumprecht, H; Beierkuhnlein, C (2014) Biotische Interaktionen im Klimawandel. In: Auswirkungen des Klimawandels auf Fauna, Flora und Lebensräume sowie Anpassunsgsstrategien des Naturschutzes, *Naturschutz und Biologische Vielfalt*, **137**, (eds C. Beierkuhnlein et al.), 212-273, Bundesamtes für Naturschutz, Bonn,

Backhaus S, Kreyling J, **Grant K**, Beierkuhnlein C, Walter J, Jentsch A (2014) Recurrent mild drought events increase resistance toward extreme drought stress, *Ecosystems,* **17**, 1068-1081

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Schuerings, J; Beierkuhnlein, C; **Grant, K**; Jentsch, A; Malyshev, A.; Penuelas, J; Sardans, J; Kreyling, J (2013) Absence of soil frost affects plant-soil interactions in temperate grasslands, *Plant and Soil,* **371**, 559-572

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Jentsch, A; Kreyling, J; Schmid, N; **Grant, K**; Gommola, J; Beierkuhnlein, C (2008) Dürre und Starkregen verschieben Blühphänologie und Produktivität von Pflanzen - ein Klimaexperiment zur Auswirkung extremer Wetterereignisse auf Biodiversität und Ökosystemfunktionen, *Naturschutz und Biologische Vielfalt*, **60**, 81-86, Bundesamtes für Naturschutz, Bonn

9 Overview of conference contribution

An overview of the conference contributions of my research as oral presentations or as posters that I have given at national and international scientific conferences are listed in Table 2.

Table 2 Own presentations of my research given at national and international scientific conferences

Date	Organization	Conference and location	Titel	Type
7/2014	Bayreuth Center of Ecology and Environmental Research (BayCEER)	8th International Symposium on Ecosystem Behavior, Bayreuth, Germany	Climate change manipulations alter biodiversity and biogeochemistry of a temperate grassland community	talk
8/2012	Ecological Society of America (ESA)	97th Annual Meeting, Portland, Oregon, USA	Community shifts in grassland due to more extreme intra-annual precipitation variability and warming	talk
9/2011	Ecological Society of Germany, Austria and Switzerland (GfÖ)	41th Annual Meeting, Oldenburg, Germany	Increased intra-annual precipitation variability: how to conserve forage quality	talk
9/2011	European Ecological Federation (EEF)	12th Congress, Avila, Spain	(No) community shifts in grassland due to more extreme intra-annual precipitation variability	poster
8/2011	Ecological Society of America (ESA)	96th Annual Meeting, Austin, Texas, USA	Sensitivity of plant functions (i.e. growth, photosynthesis, phenology) and community composition in temperate grassland to severe drought	talk
8/2011	Ecological Society of America (ESA)	96th Annual Meeting, Austin, Texas, USA	Increased intra-annual precipitation variability affects biomass production and forage quality	poster
9/2010	Ecological Society of Germany, Austria and Switzerland (GfÖ)	40th Annual Meeting, Giessen, Germany	Effects of intra-annual rainfall variability on productivity of semi-natural grassland communities	talk
5/2010	European Geoscience Union (EGU)	General Assembly 2010, Vienna, Austria	Resilience of aboveground productivity in the face of reoccurring drought events	poster
4/2010	Botanical Society of Scotland	International conference on Phenology: Plant ecology and diversity, Edinburgh, Scotland	Beyond gradual warming - extreme weather events alter flower phenology of European grassland and heath species	talk
9/2009	Ecological Society of Germany, Austria and Switzerland (GfÖ)	39th Annual Meeting, Bayreuth, Germany	Mechnismusm behind stability - productivity of grassland communities remained surprisingly unaffected under annual reoccurring extreme weather events	talk
4/2009	Bayreuth Center of Ecology and Environmental Research (BayCEER)	BayCEER Workshop, Bayreuth, Germany	Drought and heavy rainfall alter biotic interactions among plants	talk

10 Summary

The Earth's climate is increasing in its variability as a consequence of global warming. Therefore, it is important to develop a better understanding how ecosystems, especially grassland, may respond to increased climate variability. The following thesis presents potential impacts of increased intra-annual climate variability on the productivity, forage quality, and plant community composition of mesic temperate grassland. Possible interactions of multiple climate factors – precipitation variability and seasonal warming – are studied and underlying processes that alter the resistance and resilience of mesic temperate grassland are investigated. In particular, this thesis tests management practises, namely fertilisation, cutting date, and cutting frequency, as potential tools to adapt grassland to the projected increase in climate variability.

All investigations were done using the following experimental approach: precipitation variability was manipulated in two long-term field experiments, EVENT-1 and EVENT-2, located in the Ecological-Botanical Garden of the University of Bayreuth. In EVENT-1, artificial, mesic temperate grassland with varying community composition was subjected to annually recurrent, extreme weather events (drought, heavy rainfall). In EVENT-2, semi-natural, mesic temperate grassland was subjected to altered intra-annual precipitation variability (low, medium, high). The 'high variability' treatment included either a spring or a summer drought event combined with heavy rain pulses to test for seasonality effects. Precipitation variability was tested in interaction with management practises (fertilisation, cutting regime) or seasonal warming (winter, summer) was studied.

The results of this thesis show that high intra-annual precipitation variability is decreasing the aboveground productivity of mesic temperate grassland – particularly when it coincides with low annual precipitation amounts. The seasonal occurrence of the climatic factors, early vs. late drought events or winter vs. summer warming, was neither amplifying nor buffering the observed precipitation effects on productivity. Increasing intra-annual precipitation variability led to changes in the grassland community composition favouring forbs over grasses. In contrast to findings on productivity, the interaction of the precipitation and temperature variability was an important driver for the shift in community composition, A more variable precipitation regime with spring or summer droughts coinciding with higher summer temperatures reduced species evenness. Furthermore, the changes in community composition due to a more extreme precipitation pattern and plant senescence were found to be responsible for alterations of forage quality. Increased precipitation variability caused a short-term decrease in forage quality of single plants, in terms of lower leaf nitrogen and protein concentrations. However, a general increase in the forage quality was observed at the community level in the face of high intra-annual precipitation variability.

The results of this thesis further reveal that single climatic extremes caused species specific shifts in plant–plant interactions from facilitation to competition or vice versa, and the nature of the shifts varied depending on the particular community composition. Moreover, a facilitative legume effects on neighbouring plant growth was found under ambient weather conditions and heavy rainfall events but it disappeared under extreme drought. The observed changes in plant-plant interaction and the presence of legumes could be seen as possible mechanisms that stabilise grassland community productivity in the face of increased precipitation variability.

In this thesis, management practises, which are fast and easily applicable, are tested for the first time for their suitability as adaptation tools to overcome the influence of altered intra-annual climate variability on mesic temperate grassland. More frequent cutting (4 vs. 2 cuts per year) neither buffered, nor amplified the adverse effects of rainfall variability on productivity, but made forage quality in early summer more responsive to altered rainfall patterns. In general, fertilisation enhanced forage quality, while a 10-day delayed harvest reduced forage quality. However, these practises were only partially successful at sustaining grassland productivity under increased intra-annual precipitation variability. Only fertilisation reduced losses in grassland annual yield caused by an extreme precipitation regime. The effectiveness of these practises was negatively influenced by a later seasonal occurrence of extreme weather events. Adaptation strategies have yet to be found which are also flexible enough to respond to the seasonality of extreme weather events. The alteration of the grassland communities due to increased precipitation variability indicated that a higher diversity in species and functional traits seem to have the potential to partly buffer negative effects.

In addition, this thesis includes a critical view on precipitation change experiments and gives recommendations on how to improve the integration of data from these experiments into meta-analyses and climate change models. The application of routine measurements of basic variables and an experimental design jointly developed by field ecologists and modellers would bring the largest benefit for the global change research.

Altogether, this thesis shows that mesic temperate grassland already experiences biomass losses and vegetation shifts due to increased climate variability. These changes in turn modify ecosystem services beyond productivity, for example forage quality. The mechanisms behind the resistance and resilience of this grassland are not easily identified because of the complexity of abiotic and biotic factors. This simplified experiment reveals that biotic interactions, such as competition and facilitation, and functional diversity play a key role in the response of mesic temperate grassland to the alterations in precipitation and warming pattern. Future research, such as on the assistance of ecosystem adaptation to the projected climate change, now faces the challenge to capture not only the frequency and magnitude, but also the seasonality of multi climatic factors.

11 Zusammenfassung

Die globale Erwärmung führt zu einem Anstieg der Variabilität des Erdklimas. Daher ist es notwendig, ein besseres Verständnis dafür zu entwickeln, wie Ökosysteme, insbesondere Grünland, auf eine erhöhte Klimavariabilität reagieren. Die vorliegende Dissertation stellt mögliche Auswirkungen von erhöhter, innerjährlicher Klimavariabilität auf Produktivität, Futterqualität und Artenzusammensetzung im mesisch temperatem Grünland dar. Die Interaktion von mehreren Klimafaktoren – Niederschlagsvariabilität und saisonale Erwärmung – wird betrachtet und Prozesse der Resistenz und Resilienz von mesisch temperatem Grünland untersucht. Ein besonderer Fokus liegt dabei auf möglichen Anpassungsstrategien seitens der Bewirtschaftung, z.B. ob die Düngung oder Veränderung von Zeitpunkt oder Häufigkeit des Grünlandschnittes, eine Möglichkeit darstellen um negative Effekte durch Klimavariabilität zu kompensieren.

Für die Untersuchung dieser Fragestellungen wurde ein experimenteller Ansatz gewählt: In den Freilandexperimenten EVENT-1 und EVENT-2, die sich im Ökologisch-Botanischen Garten der Universität Bayreuth befinden, wurde eine zunehmende Niederschlagsvariabilität simuliert. In EVENT-1 wurde künstlich, mesisch temperates Grünland mit variierender Artenzusammensetzung jährlich wiederkehrenden, extremen Wetterereignissen (Dürre, Starkregen) ausgesetzt. In EVENT-2 wurde die Reaktion von semi-natürlichen, mesisch temperatem Grünland auf veränderte innerjährliche Niederschlagsvariabilität (gering, mittel, hoch) getestet. Die Variante ‚hohe Niederschlagsvariabilität' umfasste u.a. entweder eine Dürre im Frühling oder im Sommer, jeweils gefolgt von einem Starkregenereignis, um den saisonalen Einfluss von Wetterereignissen zu testen. Die Niederschlagsvariabilität wurde in EVENT-2 weiterhin mit den Faktoren Bewirtschaftung (Düngung, Schnittregime) oder saisonale Erwärmung (Winter, Sommer) kombiniert.

Die Ergebnisse dieser Arbeit zeigen, dass hohe innerjährliche Niederschlagsvariabilität die oberirdische Produktivität von mesisch temperatem Grünland verringert, insbesondere dann, wenn sie zusammen mit geringen jährlichen Niederschlagssummen auftritt. Das saisonale Auftreten von Klimafaktoren, frühe vs. späte Dürre und Winter- vs. Sommererwärmung, hatte weder verschärfende noch puffernde Wirkung auf die bereits durch Niederschlagsvariabilität veränderte Produktivität. Der Anstieg der innerjährlichen Niederschlagsvariabilität führte zu einer Verschiebung der Artenzusammensetzung im Grünland: Kräuter zeigten einen Anstieg, Gräser jedoch einen Abfall der oberirdischen Produktivität. Im Gegenteil zu den Auswirkungen auf die Produktivität war die Interaktion von Niederschlags- und Temperaturvariabilität ein wichtiger Verursacher der Verschiebung in der Artenzusammensetzung: höhere Niederschlagsvariabilität erniedrigte die Artengleichverteilung, wenn sie mit hohen Sommertemperaturen zusammentraf.

Weiterhin zeigte sich, dass die Veränderung der Artenzusammensetzung und die Seneszenz durch das variierte Wetterregime verantwortlich für Futterqualitätsunterschiede waren. Erhöhte innerjährliche Niederschlagsvariabilität verursachte eine Kurzzeitreduktion der Futterqualität von einzelnen Arten des Grünlands in Form von reduzierten Blattproteinkonzentrationen. Jedoch stieg die Futterqualität der gesamten Pflanzengemeinschaft unter den gleichen Niederschlagszenarien an.

Die Ergebnisse zeigen ebenfalls, dass einzelne extreme Wetterereignisse artspezifische Wechsel in der Pflanze-Pflanze-Interaktion von Förderung zu Konkurrenz und umgekehrt

verursachten. Die Richtung dieses Wechsels wurde von der Artenzusammensetzung beeinflusst. Außerdem trat ein förderlicher Effekt von Leguminosen auf das Wachstum von benachbarten Pflanzen unter natürlichen Wetterbedingungen und unter dem Einfluss von wiederholten Starkregenereignissen auf. Jedoch verschwand dieser Effekt unter dem Einfluss von Dürreereignissen. Die beobachteten Veränderungen in den Pflanze-Pflanze-Interaktionen und die Präsenz von Leguminosen in der Pflanzengemeinschaft können als möglicher Mechanismus gesehen werden, der die Grünlandproduktivität im Angesicht von erhöhter Niederschlagsvariabilität stabilisiert.

In dieser Arbeit wurden einfach umsetzbare Bewirtschaftungspraktiken, auf ihre Eignung für die Anpassung des mesisch temperaten Grünlands an veränderte innerjährliche Niederschlagsvariabilität getestet. Eine höhere Schnittfrequenz (vier vs. zwei Schnitte im Jahr) konnte die negativen Niederschlagseffekte auf die Produktivität weder puffern noch verstärken, jedoch machte sie die Futterqualität des Grünlands im Frühsommer anfälliger gegenüber Niederschlagsveränderung. Düngung ließ generell die Qualität ansteigen, wohingegen ein um 10-Tage verschobener Schnitt zu einer Verschlechterung der Futterqualität führte. Diese Bewirtschaftungspraktiken waren auch nur teilweise für eine Pufferung der Produktivität gegenüber Niederschlagsveränderung geeignet, denn nur Düngung konnte den Verlust des Grünlandertrages unter einem extremen Wetterregime abschwächen. Des Weiteren wurde die Effektivität dieser Praktiken negativ durch ein später im Jahr auftretendes Dürreereignisses beeinflusst. Die Veränderung in der Artenzusammensetzung durch verstärkte Niederschlagsvariabilität weist darauf hin, dass eine höhere Vielfalt an Arten und an funktionellen Merkmalen das Potential hat, negative Effekte abzupuffern.

Zusätzlich werden in dieser Arbeit Niederschlagsexperimente kritisch betrachtet und Empfehlungen gegeben, wie die Integration von Daten aus diesen Experimenten in Meta-Analysen und Klimawandelmodellen verbessert werden kann. Die Anwendung von Routinemessungen von grundlegenden Variablen sowie die gemeinsame Entwicklung von Experimentdesigns durch Freilandökologen und Modellierern könnte den größten Gewinn für die globale Forschung des Klimawandels bringen.

Die Ergebnisse dieser Arbeit zeigen, dass eine erhöhte Klimavariabilität zu einem Rückgang der Biomasseproduktion und Vegetationsverschiebungen im mesisch temperaten Grünland führt. Diese Effekte verändern im Weiteren Ökosystemdienstleistungen jenseits der Produktivität, zum Beispiel die Futterqualität. Mechanismen, die der Resistenz und Resilienz dieses Grünlands zugrunde liegen, sind auf Grund der Komplexität der einwirkenden abiotischen und biotischen Faktoren nicht einfach zu identifizieren. Die Ergebnisse dieser Arbeit lassen aber bereits erkennen, dass biotische Interaktionen, wie Förderung und Konkurrenz sowie funktionelle Diversität eine Schlüsselrolle in der Reaktion von mesisch temperatem Grünland auf Veränderungen in Niederschlags- und Temperaturmustern haben. Künftige Forschung, z.B. um die Anpassung von Ökosystemen an den projizierten Klimawandel zu unterstützen, muss sich der Herausforderung stellen, nicht nur die Frequenz und die Magnitude, sondern auch die Saisonalität von multiplen Klimafaktoren zu erfassen.

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This thesis is dedicated to my Mum!

13 Declarations

(Eidesstattliche) Versicherungen und Erklärungen

(§ 5 Nr. 4 PromO)

Hiermit erkläre ich, dass keine Tatsachen vorliegen, die mich nach den gesetzlichen Bestimmungen über die Führung akademischer Grade zur Führung eines Doktorgrades unwürdig erscheinen lassen.

(§ 8 S. 2 Nr. 5 PromO)

Hiermit erkläre ich mich damit einverstanden, dass die elektronische Fassung meiner Dissertation unter Wahrung meiner Urheberrechte und des Datenschutzes einer gesonderten Überprüfung hinsichtlich der eigenständigen Anfertigung der Dissertation unterzogen werden kann.

(§ 8 S. 2 Nr. 7 PromO)

Hiermit erkläre ich eidesstattlich, dass ich die Dissertation selbständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe.

(§ 8 S. 2 Nr. 8 PromO)

Ich habe die Dissertation nicht bereits zur Erlangung eines akademischen Grades anderweitig eingereicht und habe auch nicht bereits diese oder eine gleichartige Doktorprüfung endgültig nicht bestanden.

(§ 8 S. 2 Nr. 9 PromO)

Hiermit erkläre ich, dass ich keine Hilfe von gewerblichen Promotionsberatern bzw. Promotionsvermittlern in Anspruch genommen habe und auch künftig nicht nehmen werde.

Bayreuth, den 08.12.2015

Kerstin Grant